THE STIMULUS SPECIFICITIES OF DIFFERENT COMPONENTS OF PATTERN-ONSET VISUAL EVOKED POTENTIALS IN MAN

by

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CONTENTS

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Abstract

The transient visual evoked potential elicited by the onset of a briefly presented pattern typically contains three major components occurring within 200ms of stimulus onset. The first of these, CI, is believed to originate in striate cortex, while the second, CII, and the third, CIII, are thought to originate in separate regions of prestriate cortex.

In this thesis a series of experiments is presented in which the sensitivity of the sources of these components to the orientation, size, colour and depth of a stimulus pattern is examined.

The amplitude of CI, the only component which can be reliably elicited by a grating stimulus, varies as a function of the orientation of a previously presented adaptation grating. Attenuation is maximal when the adaptation and stimulus gratings have the same orientation, and decreases as a function of the difference in orientation between the two. The CI amplitude elicited by a grating in the absence of an adaptation pattern is independent of the orientation of the grating.

The amplitude of all three components elicited by a checkerboard stimulus varies as a function of the periodicity of the checkerboard. Amplitude is maximal at 2.0 cycles/deg and declines with higher or lower periodicities. These sensitivity functions are skewed, amplitude declining more rapidly with high periodicities than with low. The amplitudes of CI and CII elicited by an invariant checkerboard of optimal size are also sensitive to the periodicity of a previously presented adaptation checkerboard. Attenuation is maximal when the adaptation and stimulus patterns are identical, but amplitude is almost unaffected by adaptation to a checkerboard differing in periodicity from the stimulus by 1.5 octaves. Similar functions were obtained for CI when a grating

adaptation pattern was used, and when a grating stimulus pattern was used in conjunction with either a grating or a checkerboard adaptation pattern. CII, elicited by a checkerboard, is unaffected by adaptation to a grating of whatever periodicity. CIII, elicited by a checkerboard, shows no specificity to the periodicity of either a grating or a checkerboard adaptation pattern.

Greater attenuation of the CI amplitude elicited by a vertical grating occurs following adaptation to a checkerboard with oblique check sides than to one with vertical check sides, and greater attenuation of CI elicited by a checkerboard with vertical check sides occurs following adaptation to an oblique grating than to a vertical grating. This suggests that CI is sensitive to the orientations of the fundamental Fourier components of a pattern, rather than to the edges contained in the pattern.

Size specific attenuation of CI and CII transfers interocularly. Interocular transfer is almost total in the case of CII, but partial in the case of CI, suggesting a difference in binocularity between striate and prestriate cortex.

Neither CI nor CII shows specificity to either the colour or the stereoscopic depth of an adaptation pattern.

The significance of these findings in relation to animal single unit studies and human psychophysics is discussed.

CHAPTER ONE

INTRODUCTION

1.1 Approaches to VEP recording

1.2 Component analysis of transient VEPs

1.3 Physiological and psychophysical evidence of neural specificity

1.4 Thesis aims

1.1 Approaches to VEP recording

The simplest, and for several years the most common, stimulation procedure used for eliciting VEPs involves the presentation to the subject of repeated flashes of unstructured light (e.g. Cobb and Dawson, 1960; Ciganek, 1961; Rietveld, 1963) or of a uniform field whose luminance is modulated sinusoidally in time (e.g. van der Tweel and Verduyn Lunel, 1965). However, in the light of evidence from single-unit recordings of neural activity in the cat and monkey visual systems that most neurons respond best to luminance discontinuities or edges (see section 1.2), it has since become apparent that VEPs elicited by patterned stimuli are of greater physiological significance than flash VEPs. The VEPs elicited by patterned stimuli differ markedly in waveform from those elicited by unpatterned flash stimulation but recorded in an identical manner (Spehlmann, 1965; Kulikowski and Kozak, 1967).

VEPs may also be divided broadly into two categories according to the methods of stimulation and of signal-to-noise enhancement employed (Regan, 1972). Steady-state VEPs, so called because they are recorded when the brain has settled down into a "dynamic steady-state", are evoked by a stimulus with a relatively high repetition rate (commonly 8Hz) so that responses to individual presentations overlap in time. Narrow-bandwidth filters are then used to filter out the sine component of the response which has the same frequency as the stimulus, and the remaining noise element is discarded. Having a sinusoidal waveform, the resulting VEP is easily measured in terms of amplitude and phase. If required, a Fourier analyzer may be used in place of filters to give the amplitudes of the second and subsequent harmonics of the response in addition to that of the fundamental. This method has the advantage of speed, particularly valuable in clinical applications, since amplitude can be

continuously monitored during stimulation and any changes resulting from changed stimulation are immediately apparent. In the case of luminance responses, the stimulus for steady-state VEPs usually consists of sinusoidal temporal luminance modulation of a diffuse field. If patterned stimuli are used, the pattern (e.g. a grating or a checkerboard) may either be repeatedly presented into a blank field or, more commonly, it may be continuously present but reversing repeatedly in phase by 180° so that any particular region of the stimulus is alternately black then white. The mean luminance of the whole pattern then remains constant. Pattern reversal VEPs are sensitive to the contrast and orientation of the pattern (Campbell and Maffei, 1970) and to the size of the elements therein (Regan and Richards, 1971).

Steady-state VEPs elicited by checkerboard reversal have been studied extensively since they were first described by van der Tweel and Spekreijse (1966). The approach has met with some success in describing the characteristics of the visual system. For example, by measuring the amplitude of the response to a coloured checkerboard in the presence of an adapting field of variable wavelength, Regan (1974) has plotted the spectral sensitivity curve of the visual system, and using a compensation technique involving alternate illumination of a checkerboard by lights of two different colours, Estevez et al. (1975) have plotted the spectral sensitivity of each of the three cone systems. Reversal VEPs have also been used to provide evidence for neurones sensitive to binocular disparity (Fiorentini and Maffei, 1970).

Transient VEPs, in which the stimulus is presented at a slow repetition rate so that the system returns to rest between presentations, rely on a different method of signal-to-noise enhancement. In this case the amplitude of the response picked up at the electrode is plotted

against time, or latency after onset. Responses to successive stimuli are summed by a signal averager whose sweep is locked in time to the stimulus cycle. In this way visual responses, also locked to the stimulus cycle, build up rapidly with successive sweeps of the averager, while non-visual portions of the EEG build up much more slowly. The resulting VEP waveform contains a series of component peaks of differing latency and polarity whose amplitudes can be studied independently. Like steady-state VEPs, transient VEPs may be elicited by unpatterned flashes (e.g. Tepas and Armington, 1962; Clynes et al., 1964), by the onset and offset of a pattern presented into a blank field (e.g. Spehlmann, 1965; Harter, 1971) or by pattern reversal (e.g. Halliday and Michael, 1970).

Although they are slower and less convenient to record and analyze, transient VEPs have one important advantage over steady-state VEPs. Because they contain different components of different latencies, it is possible to study the topographic distribution of individual components and so to derive their origins. Thus the activity of different regions of the cortex can be studied separately and be related to neurophysiological findings concerning the primate visual system. It has been argued (e.g. Regan, 1972, p74) that comparable information may be obtained by classifying steady-state VEPs into different frequency regions in the hope of associating different frequencies with different brain functions or anatomical regions. However, although differences between the properties of high, medium and low frequency regions have been described (e.g. Regan, 1966, 1968), little progress has yet been made in relating these differences to their physiological causes.

Progress in relating transient VEP components to specific anatomical and functional regions will now be reviewed.

1.2 Component analysis of transient VEPs

Although it is a relatively simple matter to plot the amplitude distribution of transient VEP components over the scalp by recording simultaneously from an array of electrodes, a number of obstacles to derivation of their sources exist. The relation between the potentials recorded at the scalp and their underlying cortical sources is complex due to the convoluted nature of the cortex. Not only the position of the cortical generators, but also their orientation, is critical in determining the field recorded at the scalp (Shaw and Roth, 1955; Vaughan, 1969).

The mapping of the visual field on the striate cortex in man is well established (e.g. Holmes, 1945; Brindley and Lewin, 1968) and can be inferred for prestriate cortex (association cortex) from monkey studies (e.g. Daniel and Whitteridge, 1961; Cowey, 1964; Zeki, 1974). In both areas a retinotopic projection exists, the right and left halves of the field being represented in the left and right hemispheres, respectively. In the case of the striate cortex which is located at and around the occipital pole, the lower half of the field is represented largely in the upper surface within the calcarine fissure and on the medial surface above the fissure, while the upper half of the field is represented in the lower surface of the calcarine fissure and on the medial surface below the fissure. For prestriate cortex, which lies adjacent to and surrounds the striate region, the lower part of the field is represented largely on the upper convexity of the hemisphere while the upper field is represented on the under side of the occipital lobe. The picture is complicated further by a large degree of variation of cortical folding between individuals (Polyak, 1957).

Since the VEP distribution depends on the position and orientation

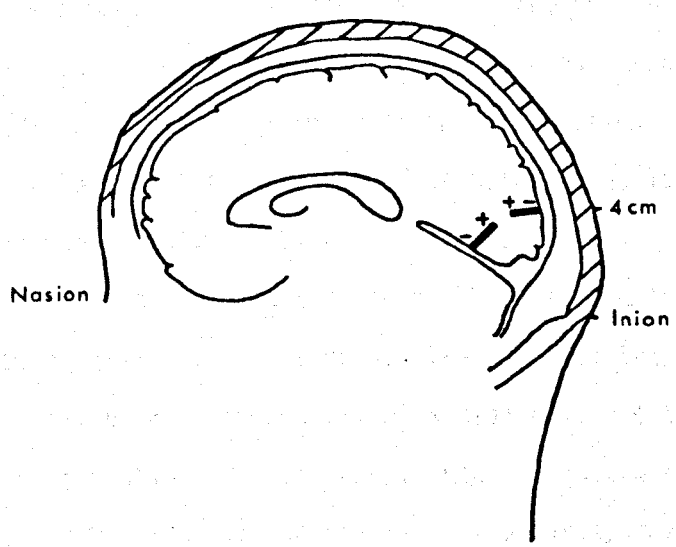
of the cortical source relative to the scalp, such anatomical variations give rise to considerable variation in the amplitudes, distributions and even polarities of VEP components between subjects.

Two attempts, one for pattern-reversal VEP components and one for pattern-onset components, have been made to identify the sources of individual components of the transient visual evoked potential. Both rest on the unproved assumptions that the cortical sources can be considered as dipoles and that the brain acts as a volume conductor (see Vaughan 1969).

Halliday and Michael (1970) have identified a component of the pattern reversal response which has a latency of about 100ms, and which is surface positive for a stimulus presented in the lower half-field and surface negative for upper half-field presentation. By separate stimulation of the octants of the visual field, these authors found that the amplitude of this component is greater for octants adjacent to the vertical meridian than for those adjacent to the horizontal meridian. This is consistent with the finding (Brindley and Lewin, 1968) that, in striate cortex, while the horizontal octants are represented within the calcarine fissure, the vertical octants are represented in the more exposed area outside the fissure. This might therefore suggest a striate origin for the 100ms reversal component. However, Halliday and Michael thought this unlikely since the maximum amplitude for both upper and lower half-field stimulation was usually recorded 5 or 7.5cm above the inion, over prestriate cortex; and in a later paper (Michael and Halliday, 1971) they proposed a model consistent with a prestriate cortical origin. In this study, they first discounted the possibility that the reversal of polarity between upper and lower half-field stimulation might arise from two distinct sets of neurones situated in the same region but whose

Fig. 1

Diagram of the medial surface of the right hemisphere showing the relative positions and orientations of hypothetical dipoles representing the prestriate cortical representation of the upper and lower halves of the visual field. Such dipole sources would give rise to VEPs of opposite polarity at an electrode 4cm above the inion. Redrawn from Michael and Halliday (1971) using the surface-negative dipoles employed in the model of Jeffreys (1971) for pattern-onset VEPs.


4 cm
Nasion
Inion

activity generates surface potentials of opposite polarity. This they achieved by showing that while the lower-field response is unaffected by a change from an ear lobe reference to a mid frontal reference, the upper field response becomes more positive. This effect is consistent with an origin in prestriate cortex on the lower surface of the occipital lobe, which is rather closer to the ear lobe than the lower field prestriate representation on the upper surface of the lobe. They then showed that if the sources are considered as dipoles, the observed polarity reversal between upper and lower field responses recorded above the inion is predicted by the difference in the orientation of the cortical surface relative to the skull surface between the lower and upper surfaces of the occipital lobe (see Fig. 1).

The analysis of pattern-onset transient VEPs into constituent components has been attempted by Jeffreys. The averaged transient VEP elicited by the onset of a patterned stimulus typically has three major components occurring within 200ms of onset. Like the pattern reversal VEP, the major pattern onset VEP components show polarity reversal between upper and lower half-field stimulation. The first component (CI, latency 75ms) and the third component (CIII, latency 150ms) usually have positive amplitude when the pattern is presented in the lower half field and negative amplitude when it is presented in the upper half field. The second component (CII, latency 110ms) usually has negative amplitude for lower and positive for upper half field stimulation (see Fig. 2). Jeffreys (1969) originally suggested that the reversal of polarity between lower and upper half field responses is best explained by the inverted orientation of the striate cortex forming the 'floor' of the calcarine fissure relative to that forming the 'roof'. However, following studies of the distributions over the scalp of the different components

Fig. 2

VEPs recorded from a transverse row of electrodes in response to stimulation of the (a) lower, (b) upper, (c) right and (d) left half-fields. Reproduced from Jeffreys and Axford (1972a).

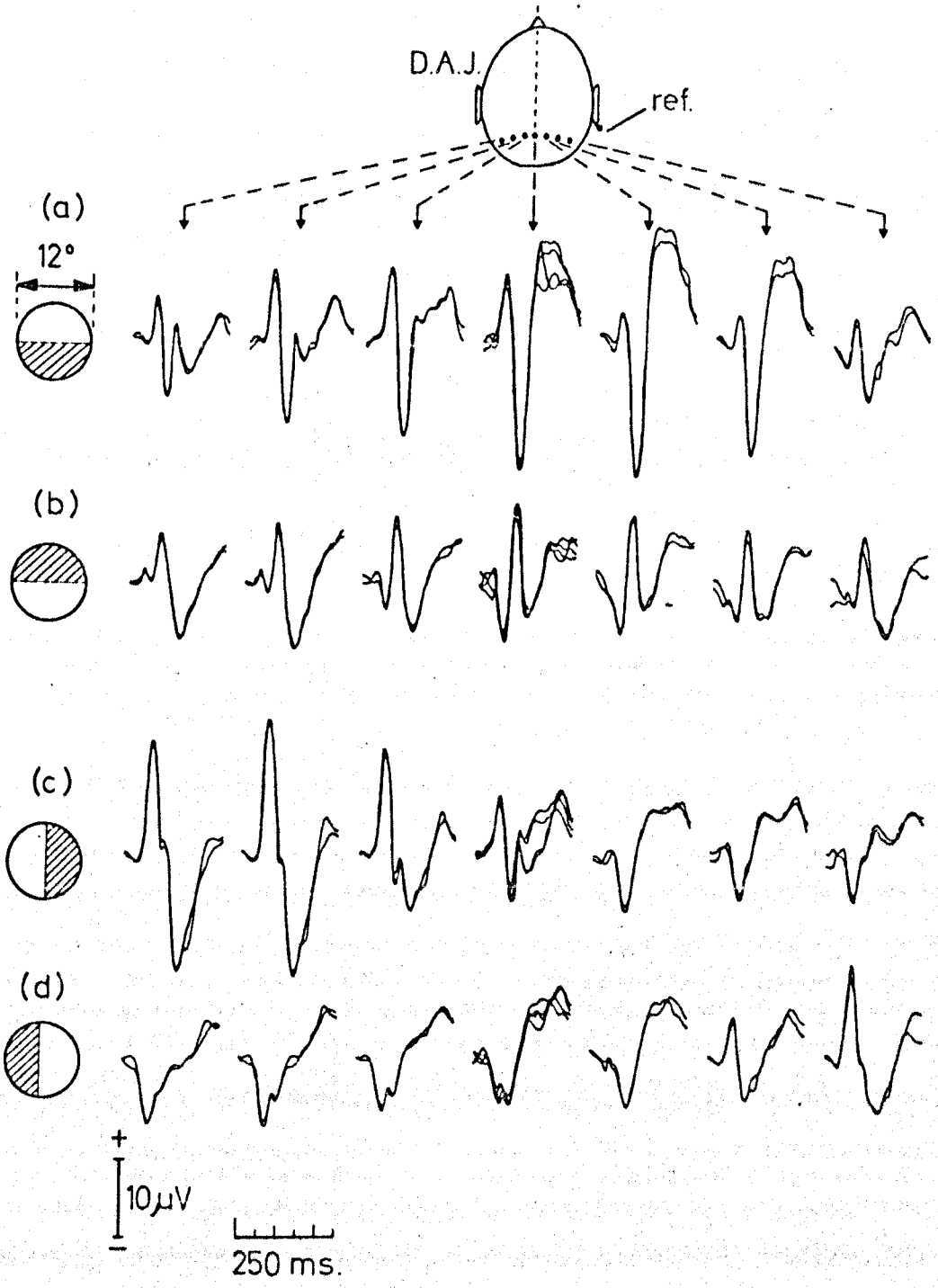
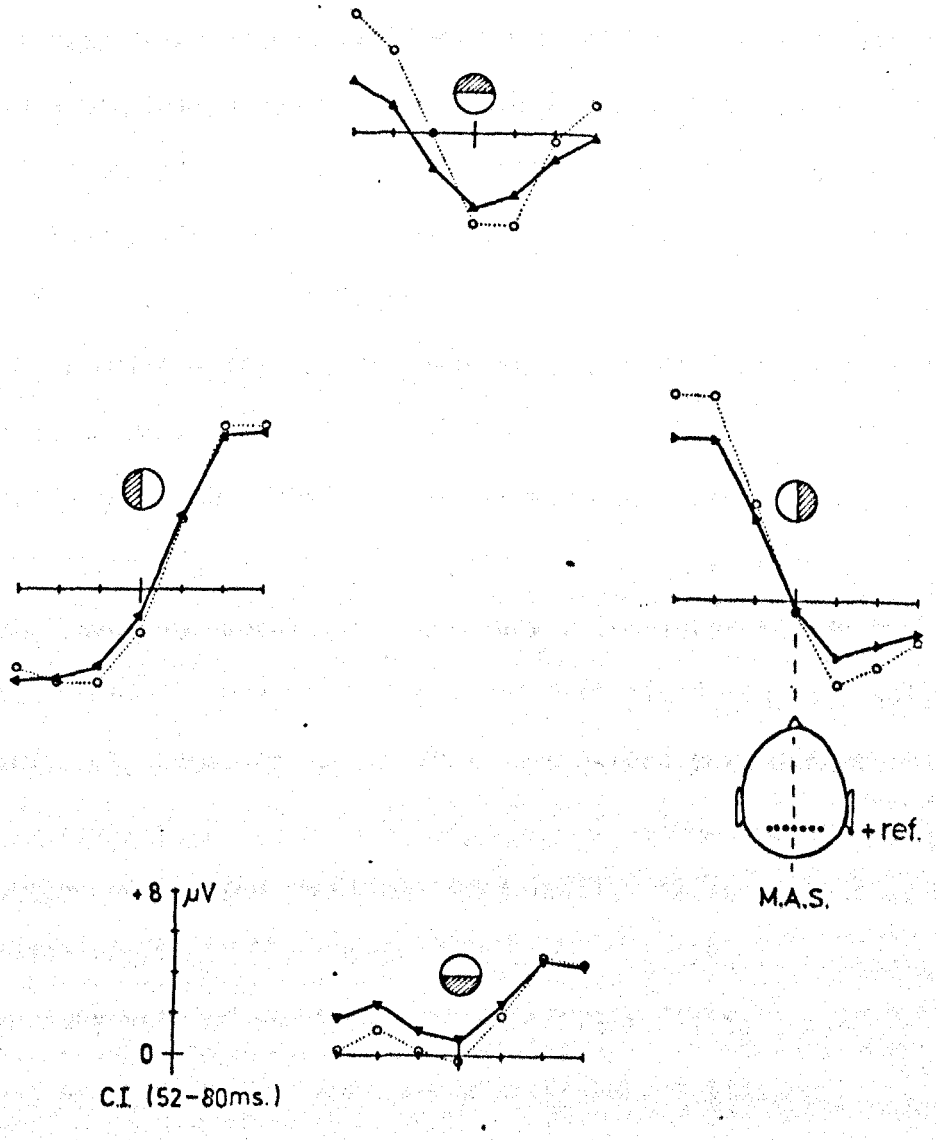

D.A.J.
ref.
(a)
12°
(b)
(c)
(d)
+
10μV
250 ms.

Fig. 3

Transverse amplitude distributions of CI for one subject for stimulation of the lower, upper, right and left half-fields. Redrawn from Jeffreys and Axford (1972a).


+ ref.
M.A.S.
+8 μV
0
C.I. (52-80ms.)

(Jeffreys, 1970, 1971a, b) it became apparent that this explanation was appropriate only to the first component (CI) and not to the later components. Jeffreys suggested instead that CII, and possibly CIII, originate in extrastriate cortex. Jeffreys and Axford (1972a) studied the variations in the amplitudes of CI and CII over a row of seven electrodes positioned horizontally across the occipital lobe, 5cm above the inion (occipital protruberance). For both components they report different distributions according to the part of the retina stimulated. Fig. 2 shows VEP waveforms for one of their subjects elicited by stimulation of the upper, lower, left and right halves of the visual field by a briefly presented regular array of squares. Fig. 3 shows, for a different subject, the amplitude of CI plotted against electrode location for the same four conditions. For upper and lower fields the distribution is monopolar, while for right and left fields it is bipolar, reversing polarity at the midline. Jeffreys and Axford showed that if the cortex is considered as a dipole sheet within a volume conducting brain, this pattern of surface amplitude distribution is consistent with a source in striate cortex. They argue that when a pattern is presented in the right or left half of the field, the potential fields generated in the floor and the roof of the contralateral calcarine fissure (representing the horizontal octants) tend to cancel out because of the inverted orientation of the cortex in the two regions. Most of the field recorded at the scalp therefore originates on the medial surfaces above and below the calcarine fissure (representing the vertical octants). Because the dipole axis of the cortex on the medial surfaces is parallel to the overlying transverse row of electrodes, the surface potential is bipolar, reversing polarity at the midline. When the pattern is presented in the upper or lower half of the field, the potential fields generated on

the medial surfaces of each hemisphere tend to cancel. Most of the surface potential field then originates within the calcarine fissures, the dipole axis is perpendicular to the electrode row, and the surface distribution is monopolar and maximal at the midline. Jeffreys and Axford substantiated these predictions by showing that, for CI, responses to stimulation of individual quadrants and octants are consistent with the model.

The bipolar surface field distribution obtained for CI with vertical half-field stimulation does not hold for CII (see Fig. 4), which in all cases has a monopolar distribution with a broad, contralateral maximum. Jeffreys (1971; Jeffreys and Axford, 1972b) suggested that CII originates in extrastriate cortex, and has explained the observed topographical amplitude variations in terms of a similar dipole model but of opposite polarity to that proposed by Michael and Halliday (1971) to explain the properties of the pattern reversal response (see Fig. 1). By recording simultaneously from ten electrodes positioned in a longitudinal row along the midline, Jeffreys (1971) plotted the longitudinal distribution of the amplitude of CII in response to a patterned stimulus in the upper and in the lower half of the field. Fig. 5a shows the distributions he obtained. Typically the lower and upper half-field distributions are both monopolar but are of opposite polarity. The lower field distribution has a maximum 2-5cm forward of the inion, while the upper field distribution peaks more anteriorly at 5-10cm forward of the inion. If the cortex is considered as a surface negative dipole sheet within a volume conducting brain, activity in the extrastriate cortex on the underside of the occipital lobe and on the upper surface of the lobe above the calcarine fissure would be expected to give rise to surface potential fields similar to those observed by Jeffreys for upper and

Fig. 4

Comparison of the transverse distributions of CI and CII for stimulation of the right and left half-fields, for four different subjects. Reproduced from Jeffreys and Axford (1972a).

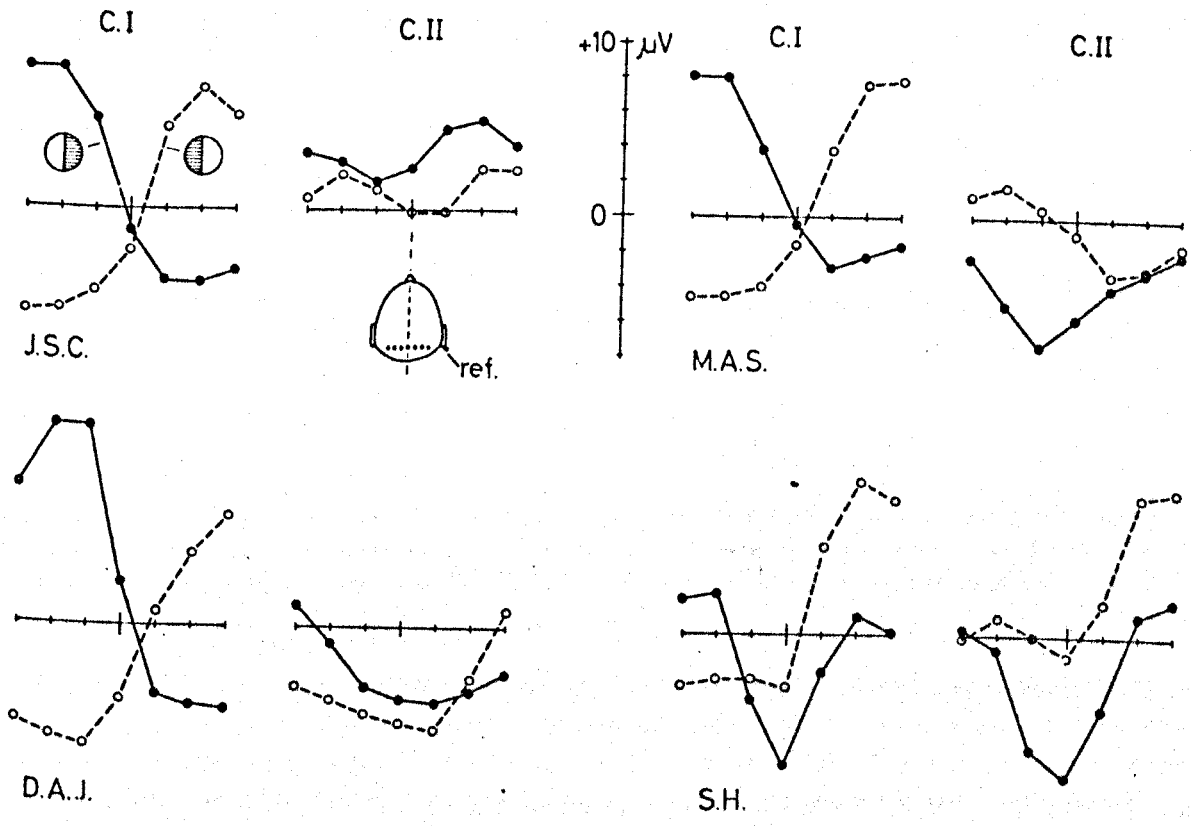
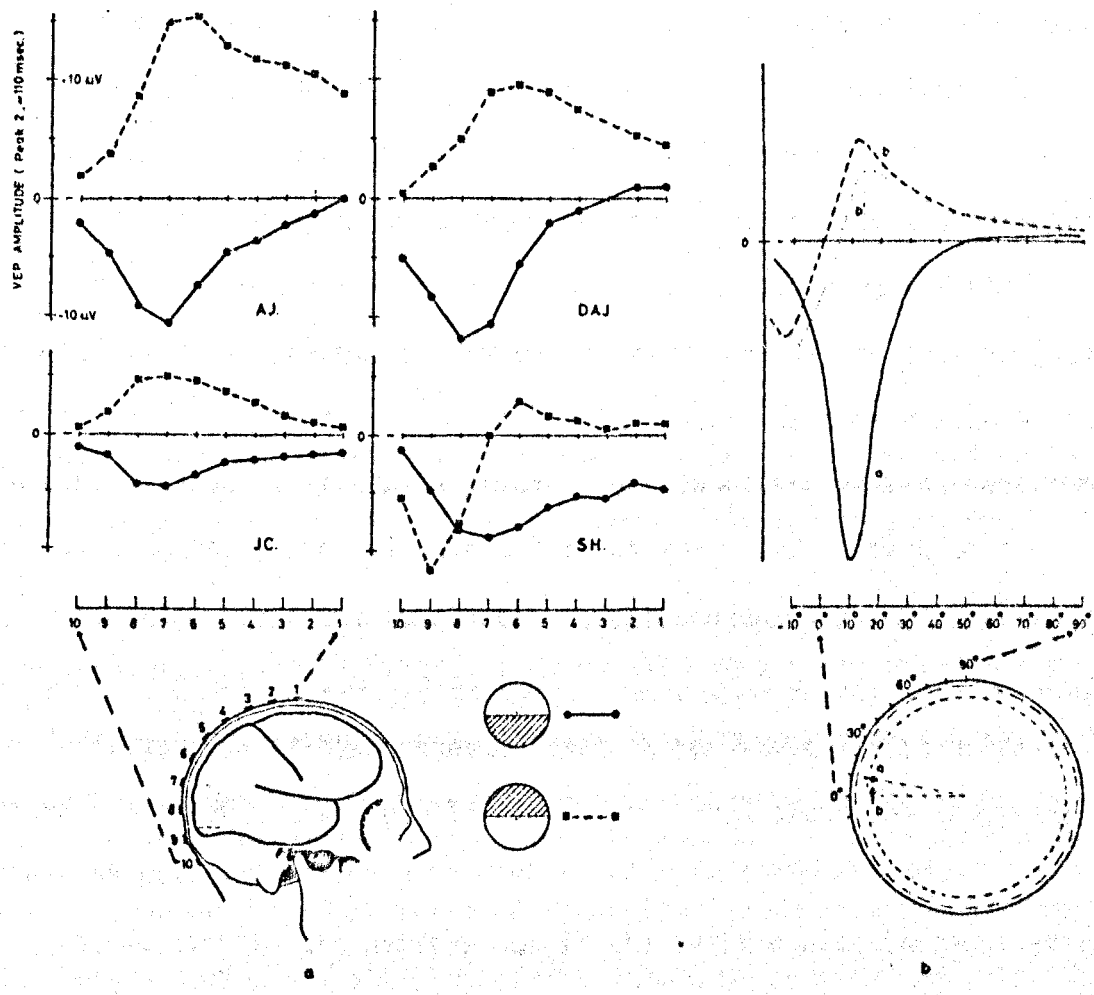

C.I
C.II
+10 μV
0
C.I
C.II
J.S.C.
ref.
M.A.S.
D.A.J.
S.H.

Fig. 5

(a) Midline amplitude distributions of CII for upper (dotted line) and lower (solid line) half-field stimulation, for four subjects. (b) Theoretical potential field distributions at the surface of a volume conducting sphere due to a single dipole at a depth 0.8R (R is the sphere radius) and oriented perpendicular to the surface (solid line), and when displaced posteriorly by 10 deg and at a depth 0.75R and oriented parallel to the surface (dashed line) and at 15 deg to the surface (dotted line). Reproduced from Jeffreys (1971).


VEP AMPLITUDE (Peak 2, ~110 msec.)
+10 uV
0
-10 uV
AJ.
DAJ
JC.
SH.
10 9 8 7 6 5 4 3 2 1
a
b
b'
a
-10° 0° 10° 20° 30° 40° 50° 60° 70° 80° 90°
90°
60°
30°
0°
b
b'
a
b

lower half-field stimulation respectively (see Fig. 5b). It seems likely, therefore, that unlike CI, which probably originates in striate cortex, CII originates in extrastriate cortex.

Considerable variation occurs in the surface distribution of VEP components for different subjects, and any model of source locations must allow for such variations. Individual variations are to be expected under the dipole model of Jeffreys, because of the known individual differences in the anatomy of the visual cortex (Polyak, 1957). Jeffreys (1971) illustrates an extreme case (subject S.H. in Fig. 5a) in which CII is negative for upper half-field as well as for lower half-field stimulation. This uncommon form can be explained if, in this subject, the posterior extremity of the calcarine fissure is some distance above the occipital pole, so that a greater portion of the extrastriate cortex representing the upper half-field lies on the upper surface of the lobe.

The third component (CIII) of the pattern onset usually has a surface distribution similar to that of CII, (but of opposite polarity), and Jeffreys (1977) has suggested that it too may arise in extrastriate cortex. However, relatively little is yet known about the properties or origin of CIII.

In addition to the differences in the surface distributions of the components, the properties of the various components differ when the conditions of stimulation are varied. The effect of such stimulus variation is best studied using constant electrode positions chosen to optimize the particular component being studied. Variations of this kind provide clues to the functional significance of the sources of VEP components. One important difference described by Jeffreys (1977) relates to threshold amplitude. For all three components amplitude is proportional to both contrast and duration up to a saturation level

beyond which it does not increase, but CII and CIII build up more rapidly with increased contrast and saturate at a lower contrast level than CI. For CII and CIII, the contrast required for amplitude saturation corresponds roughly to the level required for the outlines of the elements in the pattern to be clearly visible; for CI it corresponds roughly to the contrast level required for the subjective contrast of the elements to saturate. Another difference described by Jeffreys is in the extent of amplitude attenuation caused by pre-exposure to a pattern similar to that used to elicit the response, CII and CIII being more easily adapted than CI. CII and CIII seem to be more dependent on the outlines of the pattern than CI, which is more dependent on contrast. For example, CII and CIII are considerably attenuated by defocusing the pattern, while CI is much less affected. Also, CII and CIII are greatly attenuated by the continuous presence of a pattern of outlines, which are 'filled in' by the stimulus pattern; CI is much less affected.

The dependence of CII and CIII on outlines has led Jeffreys (1978) to suggest that CII, at least, originates in an area of prestriate cortex which is primarily specialized for processing information concerning contour and form. It is known from single unit studies of the monkey cortex (e.g. Zeki, 1974) that the prestriate cortex can be divided into a number of distinct anatomical regions, each of which is retinotopically organized and is specialized for processing one particular attribute of the visual input (e.g. colour, motion or depth). It is therefore possible that CII originates in one such region while CIII, which has a similar but not identical surface distribution, may originate in another.

1.3 Physiological and psychophysical evidence of neural specificity

It has often been argued (e.g. Barlow, 1972) that visual perception is mediated by feature-detecting cells which are selectively sensitive to specific characteristics of the visual input. These characteristics consist of local luminance discontinuities, or edges. Extensive electrophysiological investigation of the cat and monkey visual system has provided considerable evidence in support of the existence of feature-specific cells. In these studies the electrical activity of single cells in the visual system has been recorded using microelectrodes; a procedure which has seldom been possible in human subjects (but see Marg, Adams and Rutkin, 1968).

One of the most important determinants of the specificity of a given neuron is the size and shape of its receptive field. Different receptive field properties are found at different levels of visual processing. Retinal ganglion cells in the cat (Kuffler, 1953) and monkey (Hubel and Wiesel, 1960) have circular receptive fields and are maximally sensitive to spots of light or darkness. For "on" centre, "off" surround cells the firing rate of the cell is maximal when a spot of light stimulates the centre of the receptive field. Surrounding this central area of the field is an annulus where stimulation results in a reduced discharge rate. Thus a large homogeneous light stimulus covering the entire receptive field of the cell will stimulate both excitatory and inhibitory areas with little resultant net change in discharge rate. "Off" centre, "on" surround cells have the reverse receptive field organization and respond well to a dark spot in the centre of the receptive field. A similar organization to that found in ganglion cells has also been found in cells of the lateral geniculate nucleus of the thalamus in cat (Hubel and Wiesel, 1961) and monkey (Wiesel and Hubel, 1966).

In the visual cortex the most effective stimulus is not a spot but a straight edge or bar-shaped light stimulus (Hubel and Wiesel, 1959). Hubel and Wiesel (1968) have identified three major classes of these edge-sensitive cells. Simple cells have long, narrow excitatory "on" areas with inhibitory "off" surrounds similar to those of retinal ganglion cells. These cells respond well to a bar-shaped stimulus falling on the central excitatory area, but excitation is cancelled out by stimulation of the inhibitory surround. Complex cells, the most common class, are also responsive to lines or edges of specific orientations. They do not show the separation of excitatory and inhibitory regions characteristic of simple cells, but respond well to an appropriately oriented edge in any part of the receptive field. Hypercomplex cells have the same characteristics as complex cells but in addition respond only to lines of a particular maximum length. More recently, Dreher (1972) has reported that two types of hypercomplex cell exist, type 1 having inhibitory sidebands similar to those of simple cells, type 2 resembling the hypercomplex cells of Hubel and Wiesel (1968).

The bar-shaped receptive field of units in the visual cortex allows sensitivity to the orientation of a stimulus (Hubel and Wiesel, 1962, 1968; Campbell, Cleland, Cooper and Enroth-Cugell, 1968). In addition, cortical units may be selectively sensitive to direction and velocity of motion (Hubel and Wiesel, 1962, 1968; Pettigrew, Nikara and Bishop, 1968), spatial frequency (Campbell, Cooper, Robson and Sachs, 1969; Campbell, Cooper and Enroth-Cugell, 1969), retinal disparity (Barlow, Blakemore and Pettigrew, 1967) or wavelength (Gouras, 1970, 1974). Single units respond selectively to different values on these dimensions and are generally finely tuned. In the case of orientation, for example, a given cell responds maximally to one particular value and becomes less

responsive as the orientation of the stimulus is changed in either direction from the preferred value. Typically the cell will give no response to a line differing by more than about 30° from its preferred orientation (Hubel and Wiesel, 1965; Henry, Bishop, Tupper and Dreher, 1973). A single line stimulus will elicit responses from many cells differing in preferred orientation, the magnitude of the response being an inverse function of the difference between the preferred orientation and the orientation of the stimulus. The perceived orientation of a line is assumed to be related to the peak of the distribution of activity across all the orientation-specific units which respond to the line.

There are two situations where the weighting or peak of this average response can be shifted so that the apparent orientation of a line stimulus is changed. It has been suggested (Andrews, 1965; Blakemore, Carpenter and Georgeson, 1970; De Valois, 1977) that orientation specific cells are not only excited by a narrow range of preferred orientations but are also inhibited by a broader range of orientations on each side of the preferred orientations, an arrangement analogous to the antagonistic signals from receptors surrounding the central excitatory area of retinal ganglion cells (Kuffler, 1953). As a consequence, when two lines of slightly different orientations are presented simultaneously, the cells excited by one line are also inhibited to some extent by the other. As a result, the two peaks of the summed distribution of activity are shifted away from each other so that the angle between the lines is perceived as greater than its physical value. This is the tilt illusion.

The second type of apparent orientation shift results from the fact that the firing rate of a given cell declines with continued stimulation by a line to which it is sensitive (Hubel and Wiesel, 1962; Maffei, Fiorentini and Bisti, 1973). This is referred to as habituation or

adaptation. After stimulation ceases, the cell's firing rate drops to below its resting discharge rate and only slowly recovers its sensitivity. It is presumably this effect which causes attenuation of the amplitudes of VEP components following pre-exposure to an appropriate pattern (see section 1.2). As a consequence of adaptation of cells sensitive to one particular orientation, if a second (test) line is subsequently presented, those cells which have been adapted by the first line will fire more slowly than they would normally. Thus the peak response of the population of orientation-specific cells shifts away from the orientation of the inspection line, and with it shifts the apparent orientation of the test line. This is the tilt aftereffect (Gibson and Radner, 1937). A further consequence of adaptation due to exposure to a line of a particular orientation is that a second line of a similar orientation presented briefly or at low luminance will produce less activity in the adapted cells responsive to it and will therefore be harder to detect (Houlihan and Sekuler, 1968). This threshold elevation is known as forward masking.

The use of these paradigms has made it possible to measure psychophysically the width of tuning of the channels or mechanisms which feature-specific units comprise. For example threshold elevation of a grating target stimulus as a consequence of exposure to a similar adaptation grating varies as a function of the difference in orientation between the two gratings. Masking is maximal when the two gratings have the same orientation and gradually decreases until the gratings are about 45° apart when the two gratings are represented by independent populations of orientation-specific cells and no masking occurs (Campbell and Kulikowski, 1966). The tilt aftereffect and the tilt illusion are maximal when the two lines or gratings are about 15° apart

and also decrease gradually up to about 45° where there is no effect (Morant and Harris, 1965; Blakemore, Carpenter and Georgeson, 1970).

The same psychophysical paradigms (aftereffect, illusion and masking) have been employed in investigations of the coding of other stimulus attributes, namely size, stereoscopic depth and direction of motion. In the spatial frequency (size) aftereffect, following inspection of a grating of bars, a subsequently presented grating comprising finer bars (higher spatial frequency) appears to be finer than it would without prior adaptation, and a coarse grating (lower spatial frequency) appears to be coarser (Blakemore and Sutton, 1969). The effect is maximal when the inspection and test gratings differ in spatial frequency by about half an octave and declines with larger or smaller differences. The effect is also contingent on the difference in orientation between the two gratings, being maximal when there is no difference and declining as the difference is increased (Blakemore and Nachmias, 1971). In addition a grating of a similar frequency is harder to detect for a period often adaptation. Such threshold elevation is maximal when the two gratings have the same spatial frequency and decreases as a function of the difference in spatial frequency between the two gratings (Pantle and Sekuler, 1969). These effects have been attributed to the adaptation of cortical cells selectively responsive not only to a range of orientations but also to a narrow range of spatial frequencies. This interpretation, which will be discussed in more detail in chapter 4, is supported by single unit evidence of the existence of such cells in cat (Campbell, Cooper and Enroth-Cugell, 1969) and monkey (Campbell, Cooper, Robson and Sachs, 1969). The demonstration of a size illusion (MacKay, 1973) in which a grating appears coarser if surrounded by a fine grating than if surrounded by a coarse one, indicates that lateral interactions

occur between spatial frequency channels analogous to those responsible for the tilt illusion.

The existence of cells selectively sensitive to retinal disparity (stereoscopic depth) in humans has similarly been implicated using aftereffect, illusion and masking paradigms. Mitchell and Baker (1973) found that the apparent depth position of a line viewed binocularly could be shifted as a consequence of prior exposure to a similar bar seen in a slightly different depth plane. The target line appears nearer to the observer following exposure to uncrossed disparity and further away following exposure to crossed disparity. In the depth illusion the apparent depth of a target is shifted as a function of the disparity of a simultaneously presented background (Richards, 1972) and in depth-specific masking the threshold for detection of a binocularly viewed target line or grating is raised as a function of the disparity of a similar pattern presented immediately before it (Blakemore and Hague, 1972; Felton, Richards and Smith, 1972). These three depth effects all show tuning functions analogous to those of their orientation and size counterparts. Masking is maximal when the inspection and test stimuli have the same disparity, the aftereffect and illusion do not occur under such conditions but are maximal at some critical difference in disparity between the two stimuli.

In the motion aftereffect, following exposure to a pattern moving steadily in one direction a stationary test pattern will appear to move slowly in the opposite direction (Wohlgemuth, 1911; Holland, 1965). This effect has been attributed to the adaptation of cortical cells responsive to spots of light moving in a particular preferred direction (Barlow and Hill, 1963a). Physiological evidence for the existence of such cells has been found in studies of the retina of the rabbit (Barlow and Hill, 1963b)

and the visual cortex of the cat (Hubel and Wiesel, 1959) and monkey (Hubel and Wiesel, 1968). The response of each motion-sensitive cell is maximal for one particular direction of movement and declines as a function of the difference between the preferred direction and that of the stimulus. The perceived direction of motion of a stimulus is assumed to be given by the peak of the distribution of activity across all direction-specific cells in the same way as its orientation is given by the distribution of activity of orientation-specific cells. Thus, following prolonged exposure to motion in one particular direction, cells responsive to that direction and adjacent directions will respond less strongly than cells responsive to other directions in the absence of any moving stimulus, and the distribution of activity will signal motion in the opposite direction. In the corresponding illusion (induced motion, or motion contrast), a stationary test pattern viewed against a moving background appears to move in the direction opposite to that in which the ground is moving (Duncker, 1938).

The psychophysical experiments cited above lend clear support to the notion that cortical units tuned to stimulus orientation, size, direction of motion and depth, of the type found in cat and monkey visual cortex, also form the basis of visual coding in man.

1.4 Thesis aims

In the preceding section, a number of psychophysical effects were described which are consistent with the known properties of single units in the mammalian visual cortex. These psychophysical experiments have the advantage that they measure the output of the entire visual system, whereas the characteristics of the activity of single units do not, and can therefore be difficult to interpret. Psychophysical procedures

therefore play an important role in providing clues to the functional significance of single unit activity.

The global nature of psychophysical measurements is at the same time a limitation, in that without complimentary single unit evidence, attempts to localize the neural basis of psychophysical effects are necessarily highly speculative.

In this thesis, an attempt is made to use visual evoked potentials to provide data intermediate in generality between single unit activity and psychophysical meausres, and which can be related to both. For this purpose, two transient VEP components, CI and CII of Jeffreys and Axford (1972a, b) (see section 1.2), were selected because they have known origins in different regions of visual cortex, and because it is possible (Jeffreys, 1977; see chapter 2) to select the stimulation and recording methods to selectively enhance each component in turn, and so to study their amplitudes independently.

The approach taken to the study of CI and CII in this thesis is to employ an adaptation paradigm analogous to that used in psychophysical adaptation experiments, in the hope that the effects of adaptation on the amplitudes of CI and CII will allow a degree of localization of the neural basis of the corresponding psychophysical effect. In addition, such adaptation experiments provide detailed information concerning the stimulus specificities of the sources of the components. Whereas previous work by Jeffreys on these components has concentrated on the effects of different stimulus patterns and electrode positions, in the experiments presented here the amplitudes of components elicited by an invariant stimulus pattern under standardised recording conditions were studied as a function of the characteristics of a second, adaptation,

pattern which preceded each presentation of the stimulus pattern. In the following chapters, the specificity of amplitude attenuation of CI and CII to the orientation (chapter 3), size (chapter 4), colour (chapter 5) and depth (chapter 6) of such an adaptation pattern are described. In chapter 7 the implications of the results presented in the preceding chapters are discussed.

CHAPTER TWO

GENERAL METHODS

2.1 Stimulation

2.2 Recording

2.3 Analysis

In this chapter general methods applicable to all the experiments presented in later chapters are described.

2.1 Stimulation

Stimuli in all experiments consisted of high-contrast transparencies presented in a tachistoscope. In most cases the transparencies were prepared photographically using Kodalith ortho film, but in a few cases they were hand-drawn on tracing paper using black ink.

Two different tachistoscopes, referred to here as A and B, were used to present the stimuli. Both were constructed in the laboratory for use in experiments other than those presented here.

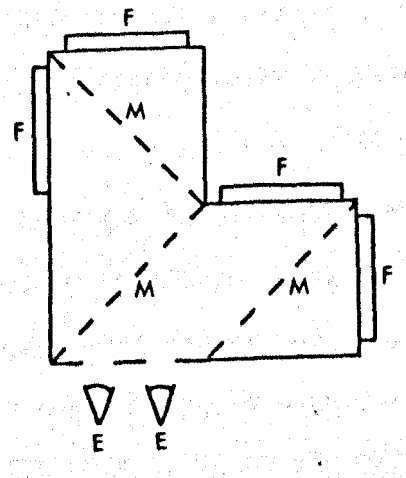
Tachistoscope A (a diagrammatic representation of which appears in Fig. 6a) had four fields which were optically superimposed by means of half-silvered mirrors. Each field consisted of an opal perspex screen, to which a stimulus transparency was attached, illuminated from behind by three 9" hot cathode fluorescent tubes (Mazda, blue, 6W) which had switching times of less than 1ms. Each field was viewed binocularly at a distance of 75cm and subtended 9 deg visual angle.

Tachistoscope B (see Fig. 6b) had five fields. Two of these were optically superimposed by means of a half-silvered mirror and presented, via a beam splitter located in front of the eye, to the subject's left eye. Two further fields were presented in a similar manner to the subject's right eye, while the fifth field could be presented, by the use of shutters, to either eye or to both eyes simultaneously. Each field consisted of an opal perspex screen illuminated from behind by two 24" hot cathode fluorescent tubes (Philips Trucolor 37) which had switching times of less than 1ms and had a suitable spectral composition for use in conjunction with coloured filters (see chapter 5). Each field was

Fig. 6

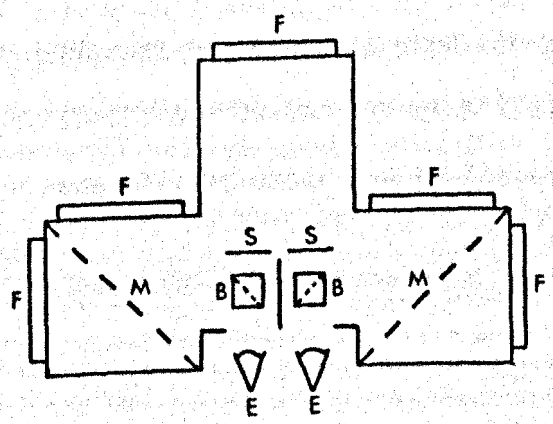
Diagrams of the two tachistoscopes, A and B, described in the text.

A



B BEAM SPLITTER
E EYE
F STIMULUS FIELD
M HALF-SILVERED MIRROR
S SHUTTER

B



viewed at a distance of 55cm and subtended 12 deg visual angle.

The switching of the tubes of both tachistoscopes was controlled by transistor bistable units triggered by a Devices Digitimer pulse generator whose timing was accurate to 0.1ms. Bistable units controlling those fields which contained stimulus patterns were triggered directly from the pulse generator. In all experiments the bistable unit controlling at least one field (usually containing only a black fixation cross) was switched on by a signal from a NAND gate and off by a signal from an OR gate, such that the field came on whenever no other field was illuminated. This ensured that there were no large changes in mean luminance during the course of the stimulus cycle. A variable resistor connected in series with the tubes of each field provided a fine control of intensity so that the luminances of the fields could be accurately matched by flicker photometry. Unless otherwise stated, the mean luminance of each field was 216 cd m^{-2} for tachistoscope A and 136 cd m^{-2} for tachistoscope B.

A variety of different patterns was used for eliciting VEPs, including gratings, checkerboards and visual noise. The actual stimuli used in each experiment will be described in the methods sections of the appropriate chapters.

In all cases, the stimuli cycled continuously during experimental runs, each cycle (of total duration between 500ms and 2000ms) containing a brief (usually 25ms) presentation of the pattern used to elicit a VEP, and sometimes also containing a longer (typically 300ms) presentation of an adaptation pattern. Where an adaptation pattern was included, a random pulse generator was used to trigger each stimulus cycle so that the inter-stimulus interval between adaptation pattern offset and test pattern onset varied randomly between 100ms and 200ms. This random

variation minimized contamination of the baseline measure (see section 2.3) by responses to the offset of the adaptation pattern.

2.2 Recording

Electrical signals were recorded from a number of electrodes (Ag/Ag Cl discs) attached to the scalp over the occipital lobe using collodion. A number of obstacles (discussed by Jeffreys, 1977) to the independent study of the VEP components CI, CII and CIII necessitated careful choice of electrode positions. One such obstacle is the temporal overlap of the various components, which makes the apparent amplitude and latency of each component dependent to some extent on the relative amplitude and polarity of the preceding and/or succeeding components (Shagass, 1972). Jeffreys (1977, p144) reports that by the choice of a suitable combination of electrode position and the position within the visual field in which the stimulus is presented, it is often possible to selectively enhance the amplitude of any one component and so minimize amplitude modification resulting from temporal overlap with other components. He illustrates how, for one subject, CI is effectively isolated by using a right half-field stimulus pattern and recording bipolarly between electrodes placed symmetrically on each side of the midline (i.e. recording between the two opposite polarity peaks of the bipolar horizontal distribution of CI (see section 1.2)). Similarly, CII and CIII could be selectively enhanced by using a lower half-field stimulus and recording from a midline electrode referred to a "neutral" point (earlobe). The separation of CII and CIII from each other is more difficult because of their very similar distributions, and was not attempted.

The choice of optimal recording conditions can differ between

subjects because of individual differences in component amplitude distributions, and ideally requires a prior knowledge of each subject's distribution characteristics. In view of the large number of subjects used in the experiments reported here (usually six in each experiment, but seldom the same six in two successive experiments) it was not feasible to obtain such information for all subjects. It was therefore decided to use standardized electrode positions and stimulus positions based on the selective enhancement technique described above, and to reject data from any subjects for whom components could not be measured more or less independently in this manner.

The following electrode configuration was used in all experiments except experiments 4 and 12 (in which pattern-reversal responses were recorded from a single active electrode situated 2.5cm above the inion, on the midline). Three electrodes were attached to the scalp in a horizontal row 4cm above the inion. The central electrode was on the midline, the others were at a distance of 5cm on each side of it. In addition, a reference electrode was attached to the right earlobe and a ground electrode was placed on the top of the head, roughly midway between nasion and inion.

For the study of CI the stimulus was presented in either the left or the right half of the field and VEPs were recorded bipolarly between the two electrodes positioned on either side of the midline. For each subject a preliminary run established whether left or right half-field stimulation produced a larger response, and the more effective half field was used for all subsequent runs. For the study of CII and CIII the stimulus was presented in the lower half of the field and VEPs were recorded from the midline electrode with reference to the earlobe electrode.

The signals were amplified by a Beckman TC high-gain multi-channel amplifier (time constant 0.3 sec, high frequency cut-off 150 Hz) and were then recorded on an FM tape recorder for subsequent off-line analysis. Successive responses to 40 presentations of the stimulus pattern were averaged (see section 1.1) on-line using a Mnemotron CAT 400B four-channel signal averager. Except in experiments 4 and 12, the responses were averaged over a 500ms period commencing 100ms prior to the onset of the stimulus.

2.3 Analysis

An X-Y plotter was used to obtain an analogue plot of amplitude against latency for each averaged response (40 presentations). In all cases two identical runs were carried out under each experimental condition and the resulting plots were superimposed to check repeatability. If repeatability was poor, a third run was conducted. The analogue plots obtained in this way allowed visual inspection of amplitude variations. In addition, digital values of the peak amplitudes occurring within specified latency regions (70ms to 90ms after onset for CI, 90ms to 120ms for CII, 150ms to 200ms for CIII), and of the mean amplitude during the 100ms immediately prior to stimulus onset were obtained. The latter was taken as a measure of the baseline amplitude and was subtracted from the amplitudes of the appropriate peaks to give measures of the amplitudes of the components. The digital readout was obtained off-line from a single averaging run for each stimulus utilizing the responses to all 80 presentations. In early experiments a digital voltmeter was used to obtain the digital values; in later experiments analysis of the averaged response was carried out by computer. When required, the latencies of the peak amplitudes of the three components could also be obtained.

Considerable variation in the amplitudes of all components was found between subjects under identical stimulation and recording conditions. Part of this variance resulted from the use of standardized recording techniques, since the electrode positions used were necessarily closer to their optimal positions in some subjects than in others. In order to facilitate the calculation of variance between experimental conditions it was therefore decided to normalize all amplitude measures. In the case of runs where the stimulus cycle contained only one pattern (that used to evoke the response) amplitude was expressed, for each component and each subject, as a percentage of the largest amplitude obtained for that component and that subject under any condition within the experiment. In the case of runs where the stimulus cycle included an adaptation pattern in addition to the stimulus pattern, the amplitude of a component under a particular adaptation condition was expressed as a percentage of the amplitude elicited during a control run in which the adaptation pattern was replaced by a uniform field (referred to as the unadapted amplitude).

Since most experiments had a factorial design, statistical analysis of amplitude variations was carried out by the use of analysis of variance tests.

CHAPTER THREE

ORIENTATION SPECIFICITY

3.1 Introduction

In section 1.3 evidence was reviewed which suggested that one of the primary stimulus attributes in terms of which visual information is encoded is the orientation of the stimulus elements. At the level of the visual cortex most cells have elongated receptive fields and respond only to a narrow range of orientations (Hubel and Wiesel, 1965). Psychophysical experiments were described which indicate that stimuli differing in orientation by more than about 30 deg are represented in more or less independent orientation channels, the activity of any of which can be suppressed by prolonged inspection of an appropriately oriented stimulus, leaving the sensitivity of the other channels unaffected.

In view of the generality of orientation-specificity among cells in the monkey visual cortex, it might be expected that any human VEP components which can be attenuated by prior exposure to an appropriate pattern might also show specificity of attenuation to the orientation of the pattern. Campbell and Maffei (1970) have shown that the steady-state VEP elicited by a grating stimulus reversing in phase at 8Hz can be attenuated following prolonged inspection of a similar grating. The attenuation shows an orientation tuning function similar, though rather more finely tuned, to psychophysically obtained orientation tuning functions. In Experiments 1 and 2, described in this chapter, the orientation specificities of the transient VEP components CI and CII are examined.

An interesting feature of orientation analysis is the greater acuity found in many animals, including man and monkey, for lines which are vertical or horizontal as opposed to oblique. This has often been called the oblique effect (Appelle, 1972). One explanation which has been

proposed is that fewer cortical cells are tuned to oblique orientations than to vertical and horizontal, and Pettigrew, Nikara and Bishop (1968) have reported that this is the case for cat striate simple cells in the central 5 deg of vision. Rose and Blakemore (1974), on the other hand, found no difference in the numbers of cells tuned to different orientations, but reported differences in the breadth of tuning of cells tuned to oblique orientations and to horizontal and vertical.

The amplitude of the steady-state VEP elicited by a grating reversing in phase has also been shown to be greater for vertical and horizontal gratings than for oblique. (Maffei and Campbell, 1970; Freeman and Thibos, 1978; Frost and Kaminer, 1975), providing further evidence of a neurophysiological difference between orientation channels. A similar effect has been observed in evoked potentials recorded from monkey striate cortex (Mansfield and Ronner, 1978). Yoshida, Iwahara and Nagamura (1975) have shown that the later components (190ms to 279ms) of the transient VEP elicited by a grating show comparable amplitude variations. In Experiment 3 of this chapter the effect of orientation on the transient VEP components CI and CII is examined to see whether a similar amplitude reduction at oblique orientations is found. In Experiment 4 the effect of orientation on the reversal VEP is considered.

3.2 Experiment 1: The specificity of CI to the orientation of an adapting grating.

In this experiment the adaptationparadigm described in section 2.1 was used to study orientation specificity using grating stimuli. Since CII cannot be reliably elicited by grating stimuli, the experiment was confined to the study of CI.

Procedure

Six subjects with normal or corrected acuity were used. The stimuli were presented binocularly in tachistoscope A. The test pattern was a vertical square wave grating of spatial frequency 2.0 cycles/deg presented for 25ms in the left or right half of the field (see section 2.2). The adaptation pattern, which was presented for 300ms before each test pattern presentation and was separated from it by an inter-stimulus interval which varied randomly between 100ms and 200ms, was a similar grating covering the entire field. The orientation of the adaptation pattern could be varied by rotating the transparency. Seven adaptation orientation conditions were employed ranging from 0 deg (vertical) to 60 deg in 10 deg steps (a pilot study had indicated that orientation-specific attenuation is confined to this range). The order of presentation of the seven conditions was varied randomly.

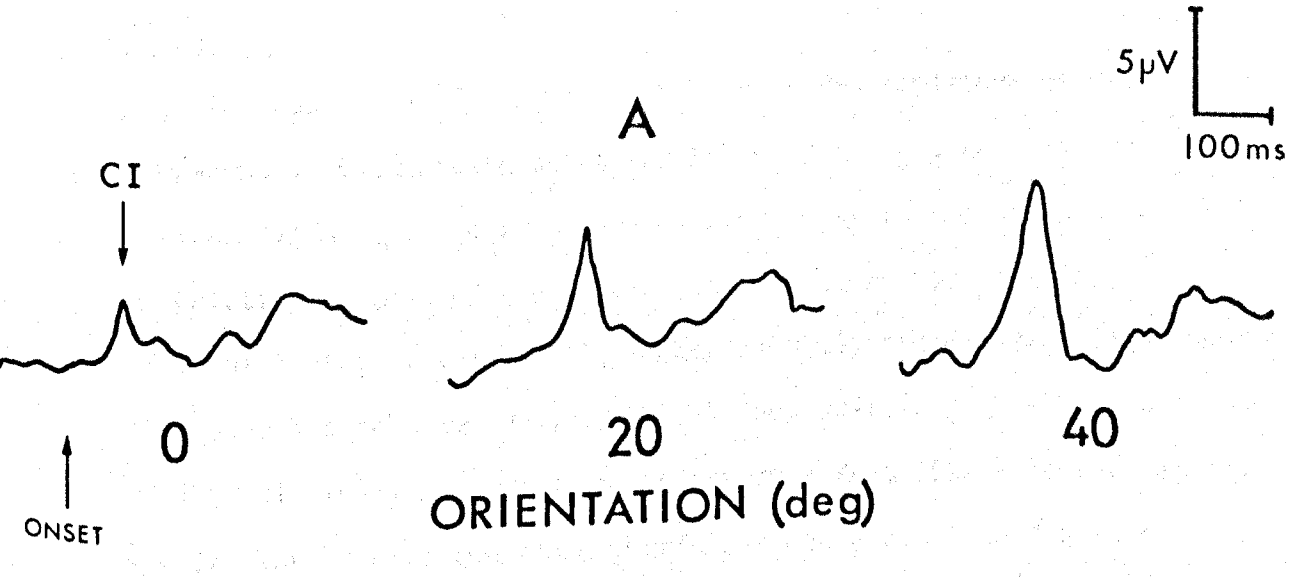
Results

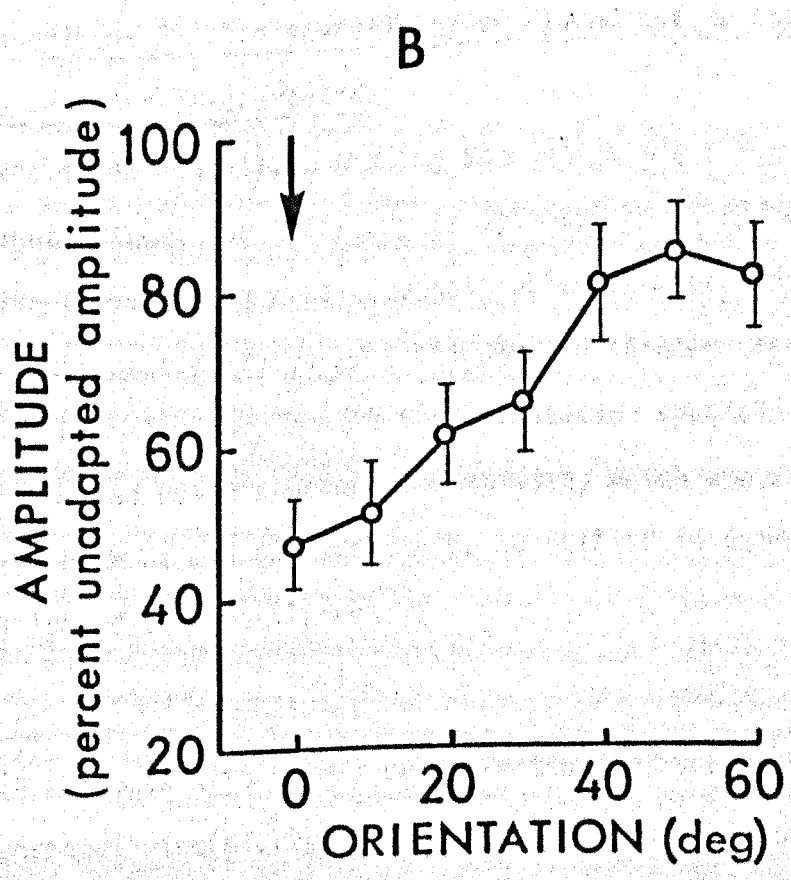
The effect of adaptation orientation on the bipolar VEP waveform recorded in the manner described in chapter 2 is illustrated for one subject in Fig. 7a. Fig. 7b shows the mean CI amplitude, for all six subjects, expressed as a percentage of the unadapted amplitude (see section 2.3), as a function of adaptation orientation. The amplitude is considerably attenuated when the adaptation grating has the same orientation as the test grating and is progressively less attenuated by increasingly different adaptation orientations up to about 40 deg when the tuning function flattens. Analysis of variance shows that amplitude is significantly affected by adaptation orientation ($F(6,35) = 6.42$, $p<.001$).

Fig. 7

(a) VEP waveforms illustrating the effect of the orientation of an adaptation grating on CI amplitude elicited by a vertical (0 deg) grating stimulus. Subject BA.

(b) Mean CI amplitude elicited by a grating stimulus pattern as a function of the orientation of an adaptation pattern.


5μV
100ms
A
CI
0
20
40
ONSET
ORIENTATION (deg)


B
AMPLITUDE
(percent unadapted amplitude)
100
80
60
40
20
0
20
40
60
ORIENTATION (deg)

Discussion

The results of Experiment 1 show that the amplitude of CI, the component of the pattern onset VEP believed to originate in striate cortex, can be attenuated by pre-exposure only to a grating of a similar orientation to that of the grating used to evoke the response. The width of tuning is similar to, though slightly broader than, that found in psychophysical studies of contrast threshold (e.g. Campbell and Kulikowski, 1966) and steady state reversal VEPs (Campbell and Maffei, 1970). The results therefore provide evidence consistent with the existence in human striate cortex of orientation-sensitive cells of the type which has been found in cat and monkey striate cortex (Hubel and Wiesel, 1965, 1968) using single-cell recording techniques.

3.3 Experiment 2: The specificity of CI and CII to the orientation of an adapting checkerboard.

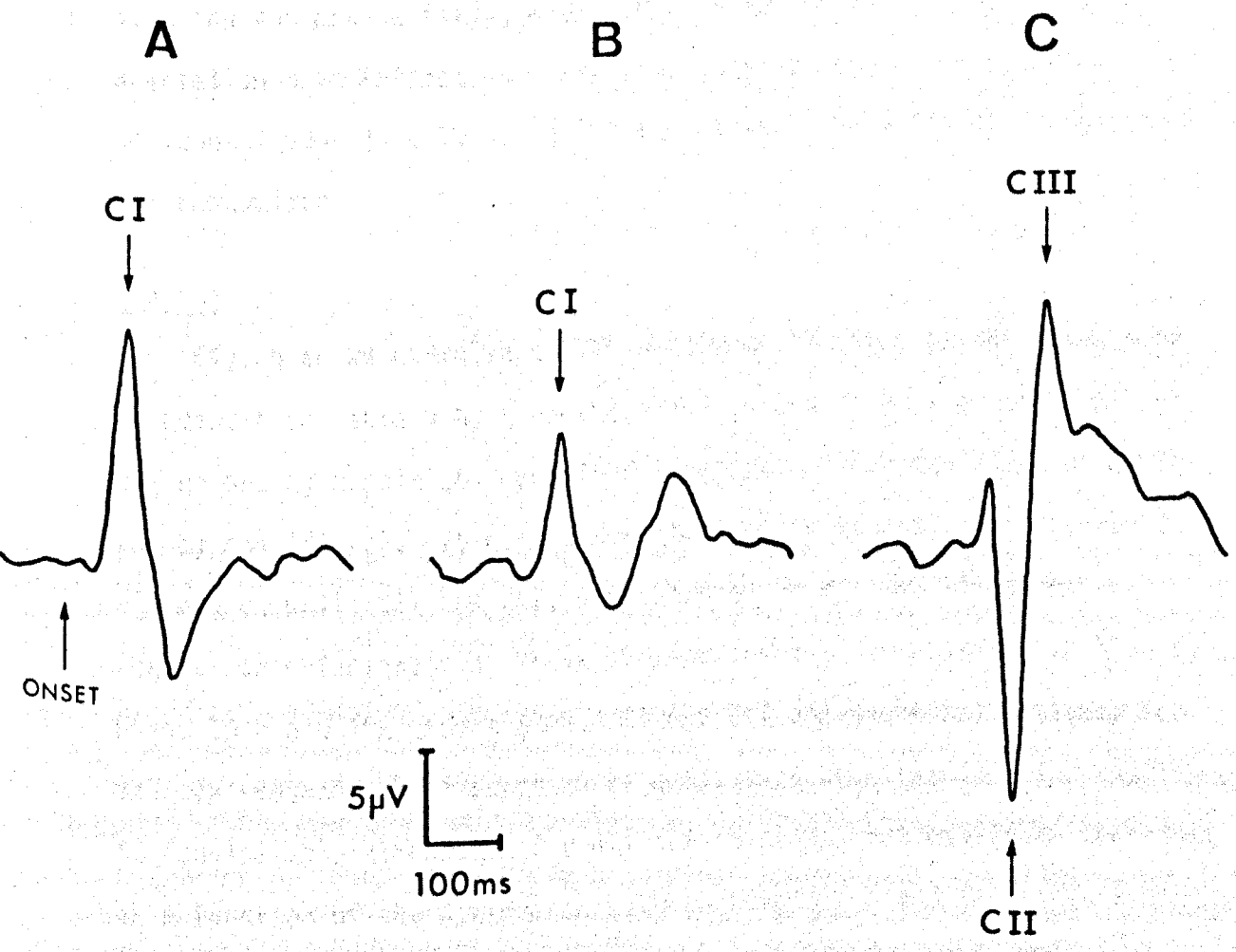
Experiment 1 utilized grating stimuli as these are the most convenient stimuli for the study of orientation specificity and are effective in eliciting a CI component which is measurable, although smaller than that elicited by a stimulus containing discrete elements (see Fig. 8). In Experiment 2 the orientation specificity of component CII is examined using checkerboard stimuli, which are effective for eliciting both CI and CII and can be quantified in terms of the orientation of the check edges.

Procedure

Six subjects with normal or corrected acuity were used. The stimuli were presented binocularly in tachistoscope A, using the same stimulus cycle as in Experiment 1. The test pattern presented in the left or right

Fig. 8

VEP waveforms elicited in the absence of an adaptation pattern by a checkerboard (a and c) or a grating (b) under the recording conditions employed for the study of CI (a and b) and CII (c). Subject D.A.J.


A
B
C
CI
CI
CIII
ONSET
5μV
100ms
CII

half-field for the study of CI or the lower half-field for the study of CII, was a checkerboard of periodicitiy 2.0 cycles/deg with vertical and horizontal check edges. The adaptation pattern was a similar checkerboard covering the entire field, whose orientation could be varied. Seven adaptation orientations were employed varying from 0 deg (vertical and horizontal edges) to 90 deg in 15 deg steps. The order of presentation was randomized.

Results

Fig. 8 shows examples of VEP waveforms elicited in the absence of an adaptation pattern by a checkerboard (a and c) or a grating (b) under the recording conditions described in chapter 2 for the study of CI (a and b) and CII (c). It can be seen that CI is selectively enhanced in a and b, while CII and CIII are enhanced in c. The effect of adaptation orientation on these VEP waveforms is illustrated in Fig. 9. Figs. 10 a and 10b show the mean CI and CII amplitude respectively for all six subjects, as a function of adaptation orientation. The amplitude is considerably attenuated for all orientations, but amplitude increases as a function of the difference between adaptation and test orientations, being maximal at or near 45 deg for both CI and CII. This orientation function does not reach significance for either CI ($F(6,35) = 0.63$, $p>.05$) or CII ($F(6,35) = 1.75$, $p>.05$).

Discussion

Because the results show non-significant tuning functions, it cannot be stated with confidence that attenuation of CII is orientation specific. However, it was shown in Experiment 1 that CI is orientation-specific, and inspection of Fig. 9 reveals slightly greater dependence on adaptation orientation for CII than for CI. It is therefore probable that the use of either a more suitable stimulus pattern or a much larger

Fig. 9

VEP waveforms illustrating the effect of the orientation of a checkerboard adaptation pattern on the amplitudes of CI (a) and CII (b) elicited by a vertically oriented checkerboard. Subject DAJ.

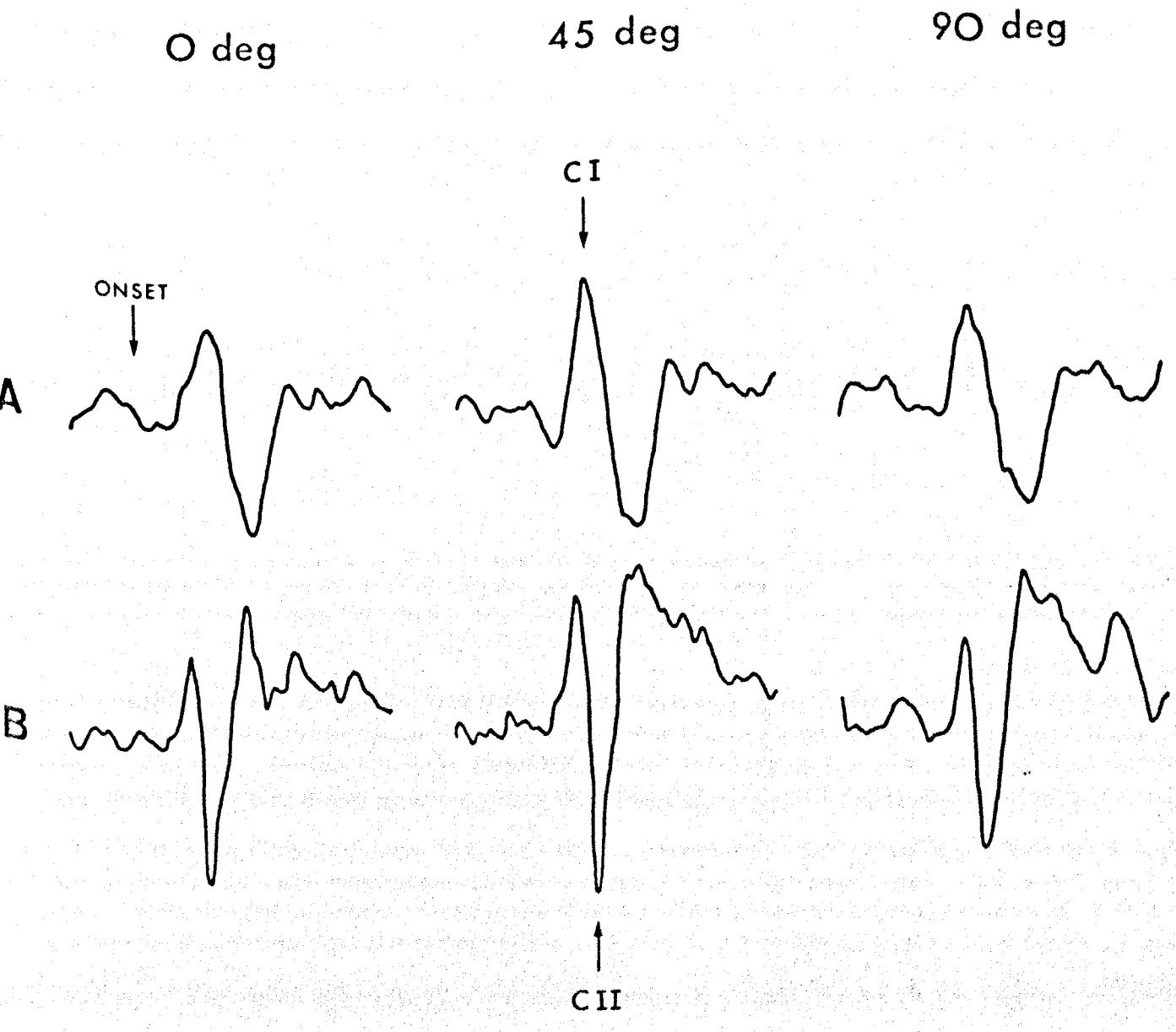
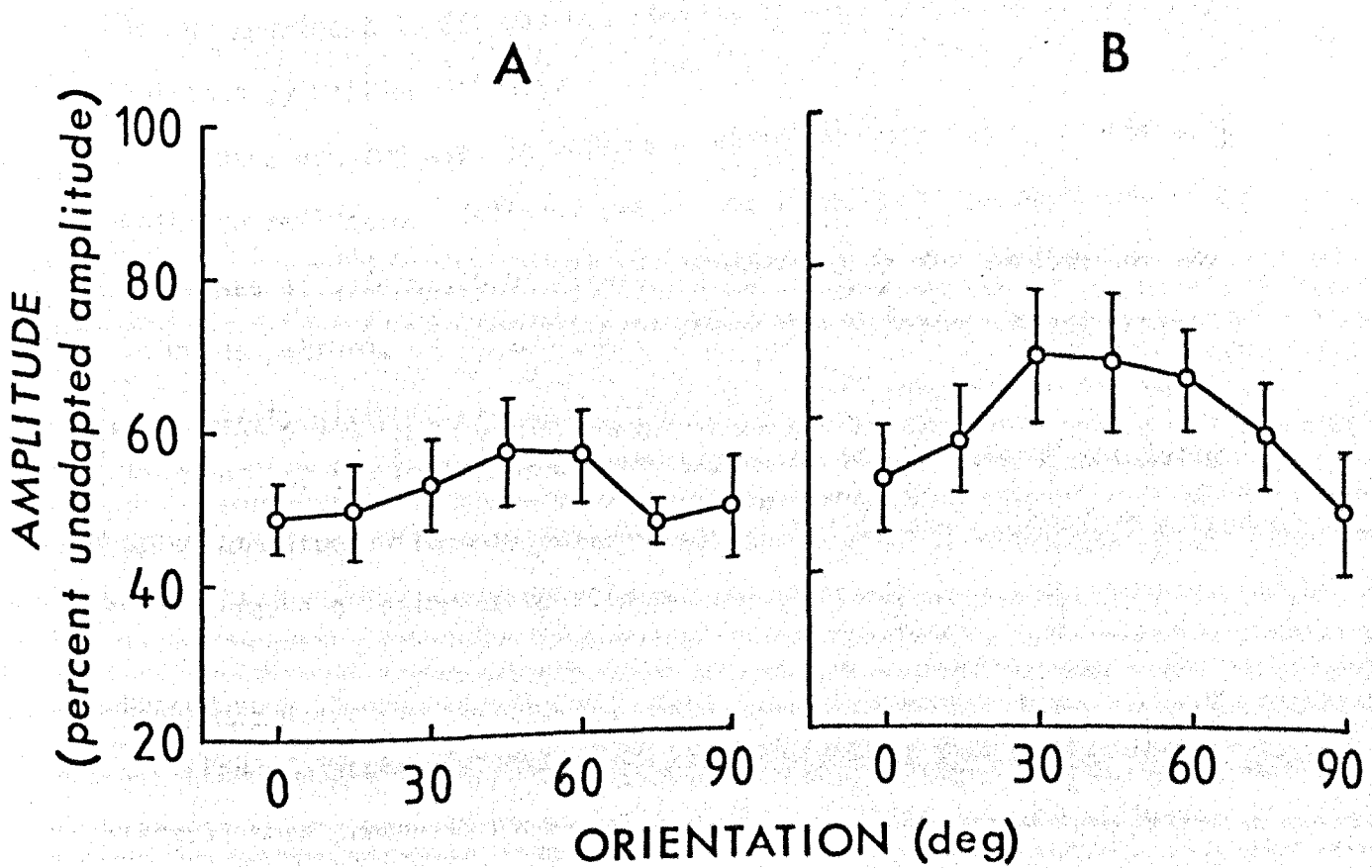

0 deg
45 deg
90 deg
CI
ONSET
A
B
CII

Fig. 10

Mean CI (a) and CII (b) amplitude elicited by a checkerboard stimulus as a function of the orientation of an adaptation checkerboard.


A
B
AMPLITUDE
(percent unadapted amplitude)
100
80
60
40
20
0
30
60
90
0
30
60
90
ORIENTATION (deg)

number of subjects would reveal significant orientation tuning for CII as well as for CI.

3.4 Experiment 3: The effect of stimulus orientation on the amplitude of CI.

In Experiment 1 it was shown that the sources of CI are orientation-specific. The aim of Experiment 3 was to see whether CI shows greater sensitivity to vertical and horizontal than to oblique grating stimuli. As in Experiment 1, CII was not studied because it cannot be reliably elicited by grating stimuli.

There are two ways in which meridional differences in sensitivity might be reflected. Jeffreys (1977) has shown that the amplitude of CI increases as a function of either the contrast or the duration of the stimulus pattern, up to about 25ms where it saturates. Meridional sensitivity differences might therefore be reflected either in the magnitude of the amplitude at saturation, or in the rate of the build up of amplitude with duration, or both. Amplitude was therefore measured over a range of stimulus durations.

Procedure

Four subjects with normal or corrected acuity were used. The stimuli were presented binocularly in tachistoscope A. The stimulus cycle (duration 600ms) contained only the pattern used to evoke the response; no adaptation pattern was used. The stimulus patterns were square-wave gratings of spatial frequency 2.0 cycles/deg presented in either the right or left half of the field. Four orientations were used: 0 deg (vertical), 90 deg (horizontal), 45 deg and 135 deg (oblique). Each orientation was presented at nine different durations ranging in

logarithmic steps from 1.5ms to 25ms, and at 50ms. The order of presentation of orientation conditions was varied across subjects according to a Latin square, and the order of presentation of durations within each orientation condition was serial.

Results and discussion

The effect of duration on CI amplitude is shown for two orientations (0 deg and 45 deg) for one subject in Fig. 11. Fig. 12 shows the mean amplitude for all four subjects as a function of duration, for all orientations. In all cases amplitude increases as a function of duration up to 25ms but shows only a slight further increase at 50ms. There is no difference in amplitude between orientations either at or below saturation. The results therefore suggest that there is no meridional variation in the sensitivity of CI of the type found by Maffei and Campbell (1970) for the steady-state reversal response.

3.5 Experiment 4: The effect of stimulus orientation on the amplitude of the reversal VEP.

In view of the failure to find a reduction in the CI amplitude elicited by oblique gratings compared to that elicited by horizontal or vertical gratings, it was decided to replicate the experiment of Maffei and Campbell (1970).

Procedure

One subject, who had previously served as a subject in Experiment 3, was used. The stimuli were presented binocularly using tachistoscope A. The stimulus cycle (duration 125ms) contained alternate 62.5ms presentations of two identical square-wave gratings which were 180 deg out of phase, so that black and white bars changed places every 62.5ms

Fig. 11

VEP waveforms illustrating the effect of stimulus duration on CI amplitude elicited by a grating for two orientations (vertical and oblique). Subject ATS.

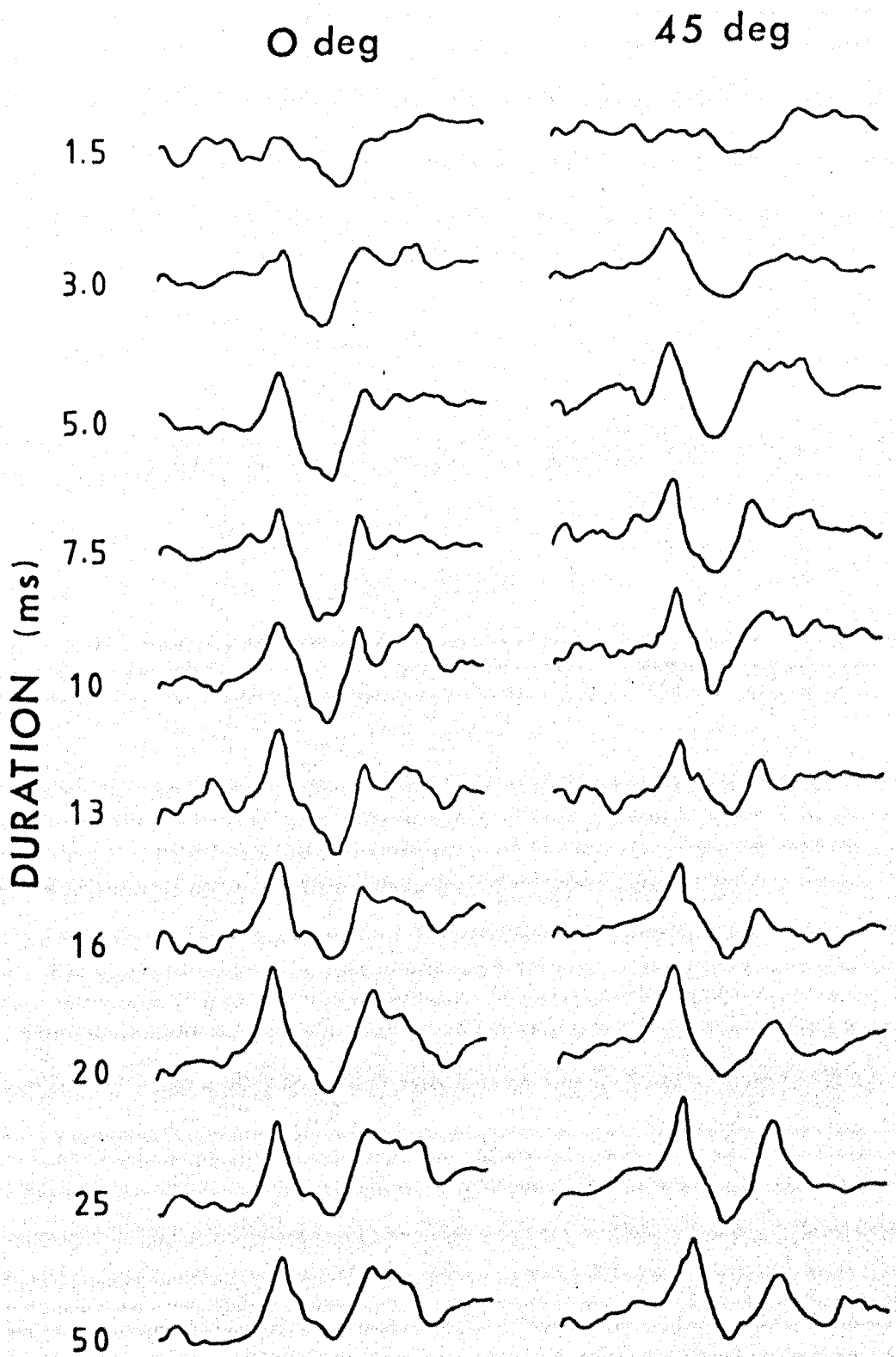
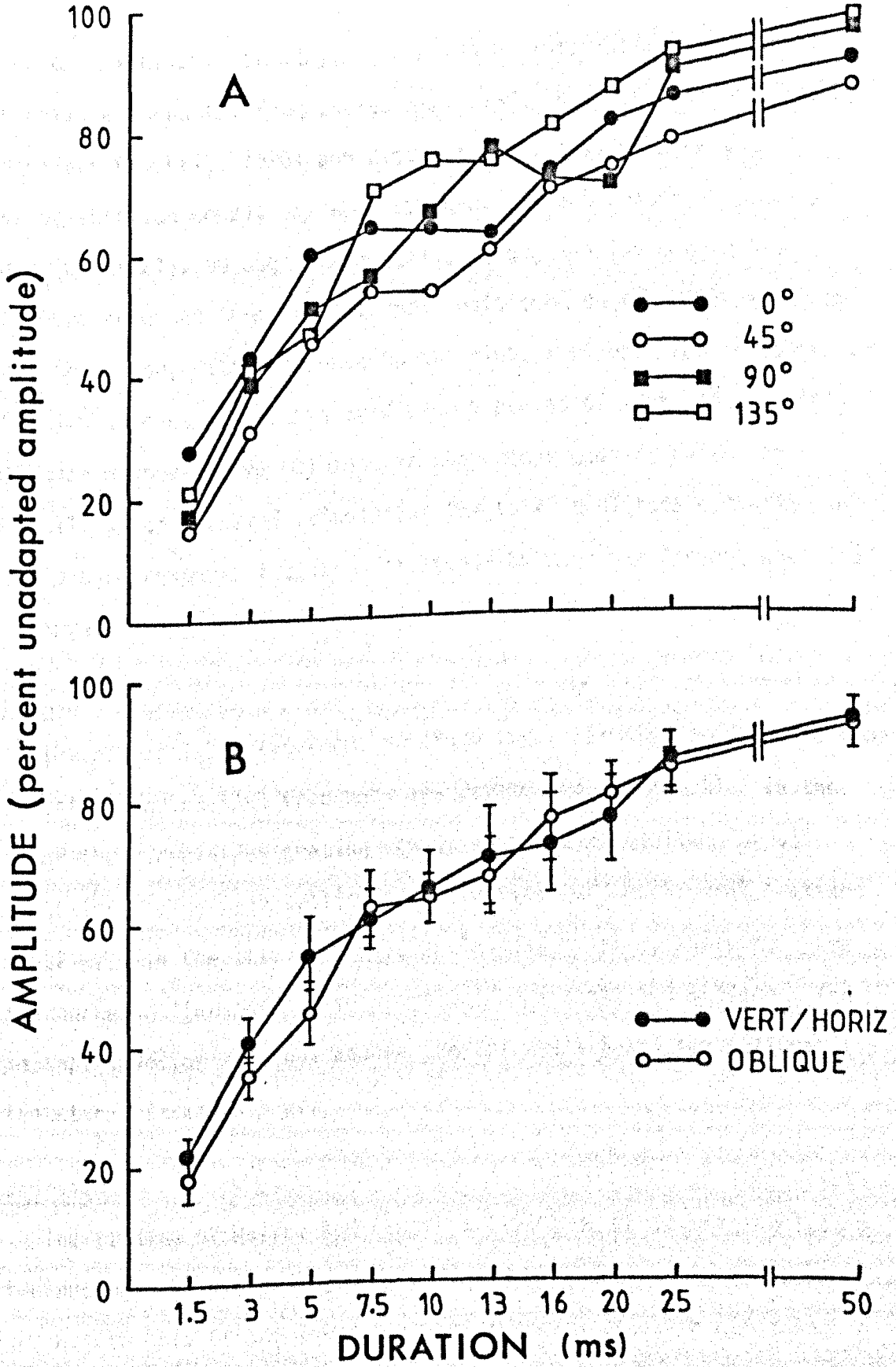

O deg
45 deg
DURATION (ms)
1.5
3.0
5.0
7.5
10
13
16
20
25
50

Fig. 12

(a) Mean CI amplitude elicited by a grating stimulus as a function of stimulus duration for four stimulus orientations. (b) The same data but showing the amplitudes elicited under oblique conditions (45 deg and 135 deg) pooled, and the amplitude under vertical and horizontal conditions pooled.


A
B
100
80
60
40
20
0
0°
45°
90°
135°
VERT/HORIZ
OBLIQUE
AMPLITUDE (percent unadapted amplitude)
1.5
3
5
7.5
10
13
16
20
25
50
DURATION (ms)

(i.e. at a frequency of 8Hz). There was no inter-stimulus interval. Two different spatial frequencies were used, 10 cycles/deg (as used by Maffei and Campbell, 1970) and 2 cycles/deg (used in Experiment 3). Four orientation conditions were employed at each spatial frequency: 0 deg (vertical), 90 deg (horizontal), 45 deg and 135 deg (oblique). VEPs were recorded from an electrode positioned on the midline, 2.5cm above the inion, with reference to the right earlobe. The responses to 200 stimulus cycles were averaged over a period of 125ms (one cycle). Amplitude measures were obtained in the manner used by Maffei and Campbell, which involved calculating the total amplitude variation in the averaged response i.e. the difference between the largest peak and the largest trough.

Results

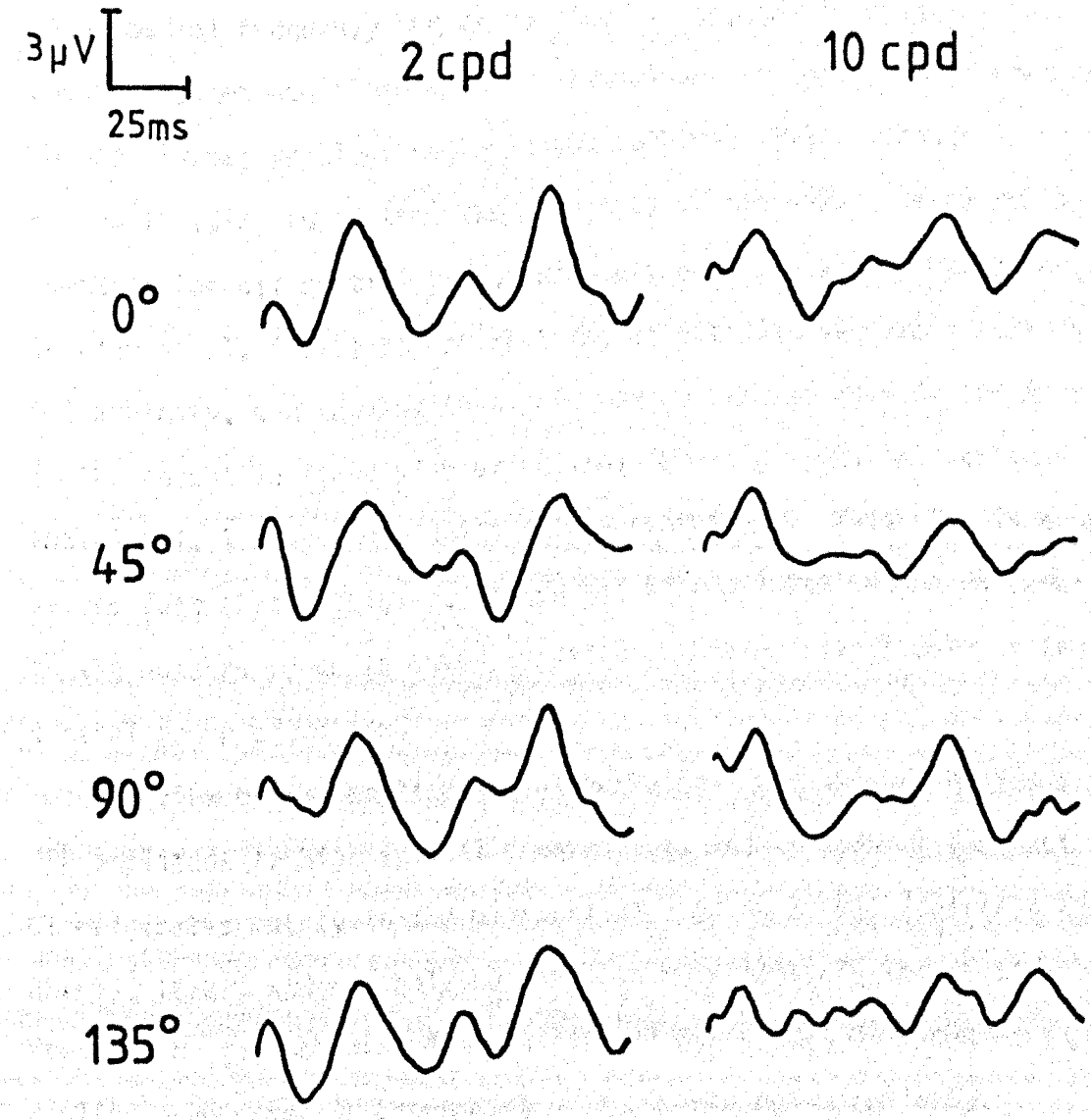
The reversal VEP waveforms recorded under all eight combinations of orientation and spatial frequency are reproduced in Fig. 13. In the case of the 2 cycle/deg grating the waveforms were similar for all orientations. The mean amplitude for vertical and horizontal gratings was 5.7 μV. In the case of the 10 cycles/deg grating, however, there was a marked difference between vertical/horizontal and oblique. The mean amplitude for vertical and horizontal was 4.5 μV; for oblique orientations it was 3.3 μV.

Discussion

The finding of Maffei and Campbell (1970) of meridional amplitude differences at 10 cycles/deg was confirmed by these results, but was shown not to hold at the lower spatial frequency used for eliciting transient VEPs in Experiment 3. This result is consistent with the finding of Freeman and Thibos (1975b) that orientation differences in

Fig. 13

VEP waveforms elicited by 8Hz phase reversal of gratings of two periodicities at each of four orientations. Subject ATS.


3 µV
25ms
2 cpd
10 cpd
0°
45°
90°
135°

the steady-state reversal VEP amplitude are more prominent at high than at low spatial frequencies.

A number of psychophysical studies have shown that the contrast sensitivity difference between oblique and non-oblique gratings increases with spatial frequency and is confined to spatial frequencies above about 5 cycles/deg (Campbell, Kulikowski and Levinson, 1966; Freeman and Thibos, 1975a; Berkley, Kitterle and Watkins, 1975) although Tyler and Mitchell (1977) found that the magnitude of the effect is approximately constant for all spatial frequencies between 0.15 and 10 cycles/deg. Berkley et al. (1975) report that the effect also decreases with retinal eccentricity, and suggest that this may be attributable to the increase in the receptive field size of retinal (Wiesel, 1960) and cortical (Hubel and Wiesel, 1962) single units with eccentricity. This view is supported by the fact that Pettigrew, Nikara and Bishop (1968) found differences in the numbers of units tuned to different orientations only in the central 5 deg of vision.

In view of the confinement of meridional variations in steady-state VEP amplitude to high spatial frequencies, and in view of the fact that CI originates mainly in the mid-periphery (2 to 6 deg) (Jeffreys and Axford, 1972a) and can only be elicited by relatively low spatial frequencies (see chapter 4), the lack of meridional differences in CI amplitude reported in Experiment 3 is perhaps not surprising.

CHAPTER FOUR

SIZE SPECIFICITY

4.1 Introduction

Considerable psychophysical evidence exists that visual processing is critically dependent on the size of the elements in the retinal image. In view of the receptive field organization of single cells in the visual system (see section 1.3), in particular the need for stimulation by an object of a particular size and shape, this is not surprising.

Campbell and Robson (1968) have suggested that the visual system is composed of many independent channels, each selectively responsive to a limited range of spatial frequencies. They based their hypothesis on the finding that the detection threshold for a square-wave grating could be predicted from the threshold for a sine-wave grating of the same periodicity, and that the contrast at which a square-wave grating could just be distinguished from its fundamental sine grating was the contrast at which its third harmonic just exceeded its own detection threshold. These experiments suggested that the fundamental and third harmonic of a square-wave grating are detected independently by separate spatial frequency channels. Subsequent studies of the detection of complex gratings (Graham and Nachmias, 1971; Sachs, Nachmias and Robson, 1971) and of spatial-frequency specific adaptation (e.g. Blakemore and Campbell, 1969) have provided further evidence consistent with such a notion.

Single units in the visual cortex of the cat (Campbell, Cooper and Enroth-Cugell, 1969) and monkey (Campbell, Cooper, Robson and Sachs, 1969) have been found which are selectively sensitive to the spatial frequency of a stimulus grating, and it has been suggested that cells of this type form the basis of spatial-frequency channels. In humans, steady-state VEPs have been used to indicate the existence of spatial frequency channels. The amplitude of the response to a grating reversing in phase at 8Hz is attenuated following pre-exposure to a grating of the

same orientation and size (Blakemore and Campbell, 1969), and the attenuation decreases as a function of the difference in spatial frequency of the test and adaptation gratings (Mecacci and Spinelli, 1976). VEP amplitude is unaffected by pre-exposure to a grating differing in spatial frequency by more than about one octave.

In Experiments 5 and 6 of this thesis the sensitivity of the transient VEP components CI, CII and CIII to the periodicity of the stimulus pattern is examined, and in Experiment 7 the amplitudes of these components of the response elicited by an invariant stimulus pattern are studied as a function of the periodicity of an adaptation pattern.

Despite the wealth of evidence which has been presented in support of the notion of visual Fourier analysis mediated by spatial frequency channels (see Sekuler, 1974; Robson, 1975, for reviews), the notion has recently been questioned. For example, King-Smith and Kulikowski (1975) have shown that the detectability of gratings can be equally well explained in terms of cells which detect single bars and that the grating contrast sensitivity function fits the prediction from probability summation between such bar detectors. MacLeod and Rosenfeld (1974) and Legendy (1975) have proposed similar models. Much of the evidence reviewed above can therefore be explained in terms either of spatial frequency channels or of bar-detectors.

However, two elegant studies have involved attempts to discriminate between these two theories, and have come to opposite conclusions. Henning, Hertz and Broadbent (1975) report that inspection of, for example, a compound grating containing three sine components of 8, 10 and 12 cycles/deg (the contrast of such a grating varies sinusoidally with a periodicity of 2 cycles/deg) impairs the visibility of a subsequently presented simple sinusoidal grating of spatial frequency 2 cycles/deg, even though

the latter grating is two octaves lower in frequency than the nearest component of the compound grating. This is inconsistent with the existence of narrowly tuned spatial frequency channels which respond to the Fourier components of a stimulus.

May and Matteson (1976) and Green, Corwin and Zemon (1976) made use of checkerboard patterns, which have major Fourier components at 45 deg to the check edges (Kelly, 1976), to show that chromatic adaptation occurs at orientations determined by the Fourier components of the adapting pattern and not by the edges present. After subjects had adapted to upright red and oblique green checkerboards, achromatic test gratings appeared pink when vertical or horizontal and green when oblique. Comparable aftereffects were observed when achromatic checkerboards were viewed after adaptation to coloured gratings. The strongest aftereffects were obtained for test gratings with a fundamental spatial frequency a factor of 1.5 above the periodicity of the adapting checkerboard; that is, close to the fundamental Fourier component of the checkerboard. These authors interpret their findings as evidence of Fourier analysis in the visual system.

The controversy is unresolved. In Experiment 8 the adaptation paradigm used in earlier experiments is used to discover whether amplitude attenuation of CI, which was shown in Experiment 1 to be orientation specific, is specific to the orientation of the fundamental Fourier components of an adaptation pattern or to the orientation of the edges contained in the pattern.

The possibility exists that the amplitude attenuation of VEP components found in the experiments presented in this and in other chapters reflects adaptation at a more peripheral stage (e.g. retina or lateral geniculate nucleus) than the cortical site from which VEPs originate. In

Experiment 9 this possibility is examined by measuring the extent to which size-specific amplitude attenuation transfers interocularly. Blakemore and Campbell (1969) found that the psychophysical grating contrast threshold measured with one eye is raised following adaptation to a similar grating in the other eye, and concluded that the adaptation must occur at least partly in binocularly driven cells in the cortex.

Studies of interocular transfer have also been used to provide an indication of the proportion of cortical cells which are binocularly driven. Movshon, Chambers and Blakemore (1972) and Mitchell and Ware (1974) report that in normal subjects the tilt aftereffect obtained with dichoptic presentation of adaptation and test patterns is reduced to 70% of the magnitude of the monoptic effect, while in stereoblind subjects, who are thought to lack binocularly driven cells, no interocular transfer is found. A similar pattern of transfer occurs for the motion aftereffect (Mitchell, Reardon and Muir, 1975) and for threshold elevation (Ware and Mitchell, 1974). These authors have argued from their findings that about 70% of the cells mediating adaptation are binocularly driven.

The same argument may be applied to the amplitude attenuation of VEP components following adaptation, and if the origins of the components are known, then binocularity can be studied independently in different cortical regions. In Experiment 10 the degree of interocular transfer of such attenuation is studied for CI and CII, in order to compare binocularity in striate and prestriate cortex.

4.2 Experiment 5: The effect of size on the amplitude and latency of CI, CII and CIII

Campbell and Robson (1968) report that psychophysical contrast sensitivity is greatest for gratings of spatial frequency about 3 cycles/

deg, and declines with higher or lower frequencies. Similar size sensitivity functions have been plotted for VEP amplitude, usually using checkerboard stimuli, but estimates of optimal check size vary between authors and between stimulation procedures (e.g. Rietveld et al., 1967; Harter and White, 1968; Regan and Richards, 1971; Armington, Corwin and Marsetta, 1971). In all cases, however, VEPs are of greatest amplitude for an intermediate range of check sizes, and are reduced for smaller and larger sizes. It has also been reported that the latencies of transient VEP components N_1-P_1 and N_2-P_2 increase with the spatial frequency of a stimulus grating (Parker and Salzen, 1977a,b). In this experiment the effect of check size on the amplitudes and latencies of components CI, CII and CIII is examined.

Procedure

Six subjects with normal or corrected acuity were used. The stimuli were presented binocularly in tachistoscope A. The stimulus cycle (duration 600ms) contained only a 25ms presentation of the pattern used to evoke the response. The stimuli were checkerboards presented in the left or right (CI) and lower (CII and CIII) halves of the field. A range of six checkerboards was used, varying in periodicity from 0.5 cycles/deg (check size 60') to 16 cycles/deg (check size 2') in one octave steps. The order of presentation was randomized. In addition to the usual amplitude measurements (see section 2.3), the latency at which the peak amplitude of each component occurred was obtained by computer analysis of the averaged response, to within 5ms.

Results and Discussion

The effect of stimulus check size on the amplitude and latency of the three components studied is shown forone subject in Fig. 14. Figs.

Fig. 14

VEP waveforms illustrating variations in the amplitudes and latencies of (a) CI and (b) CII and CIII as a function of the periodicity of a stimulus checkerboard. Subject ATS.

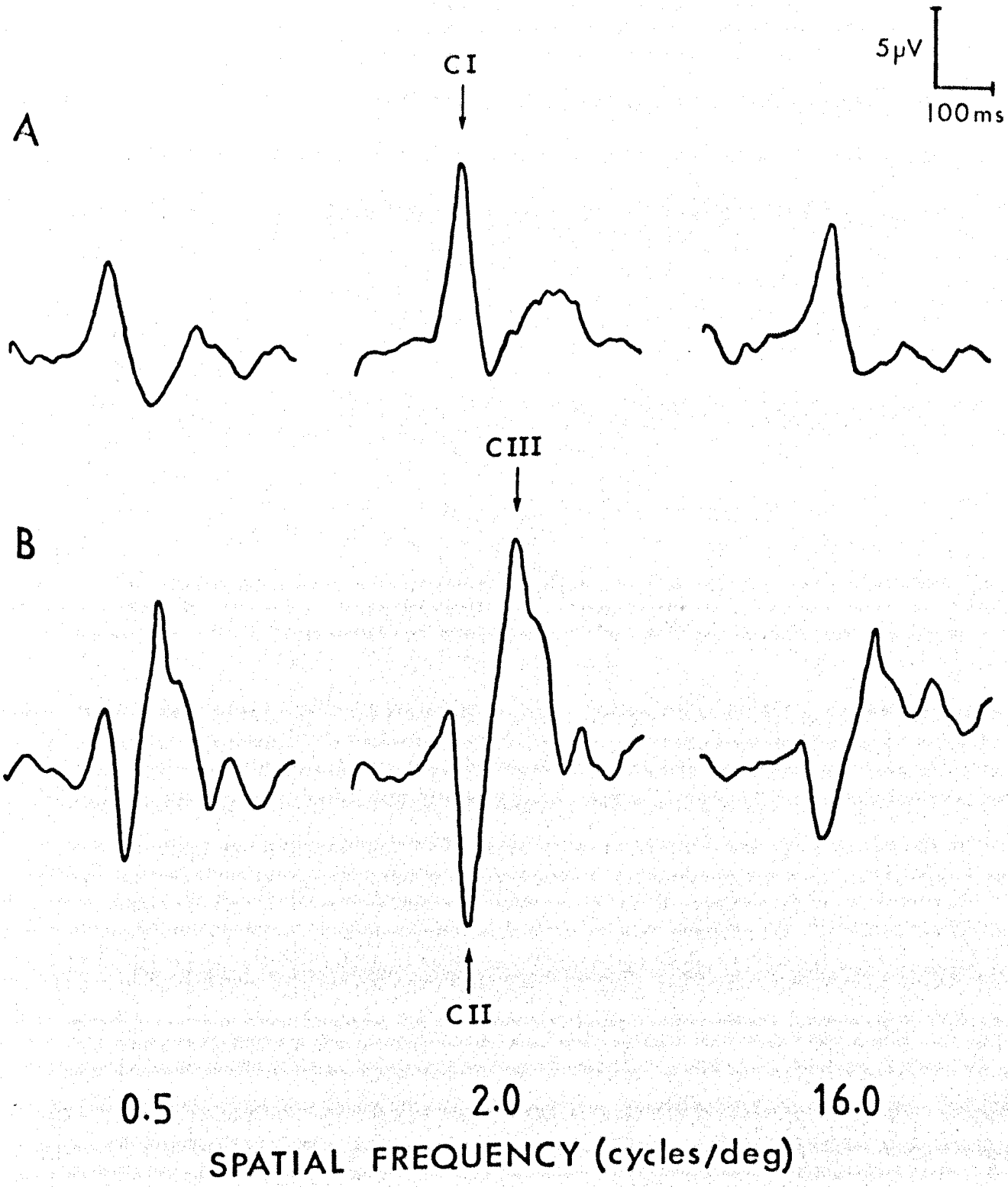
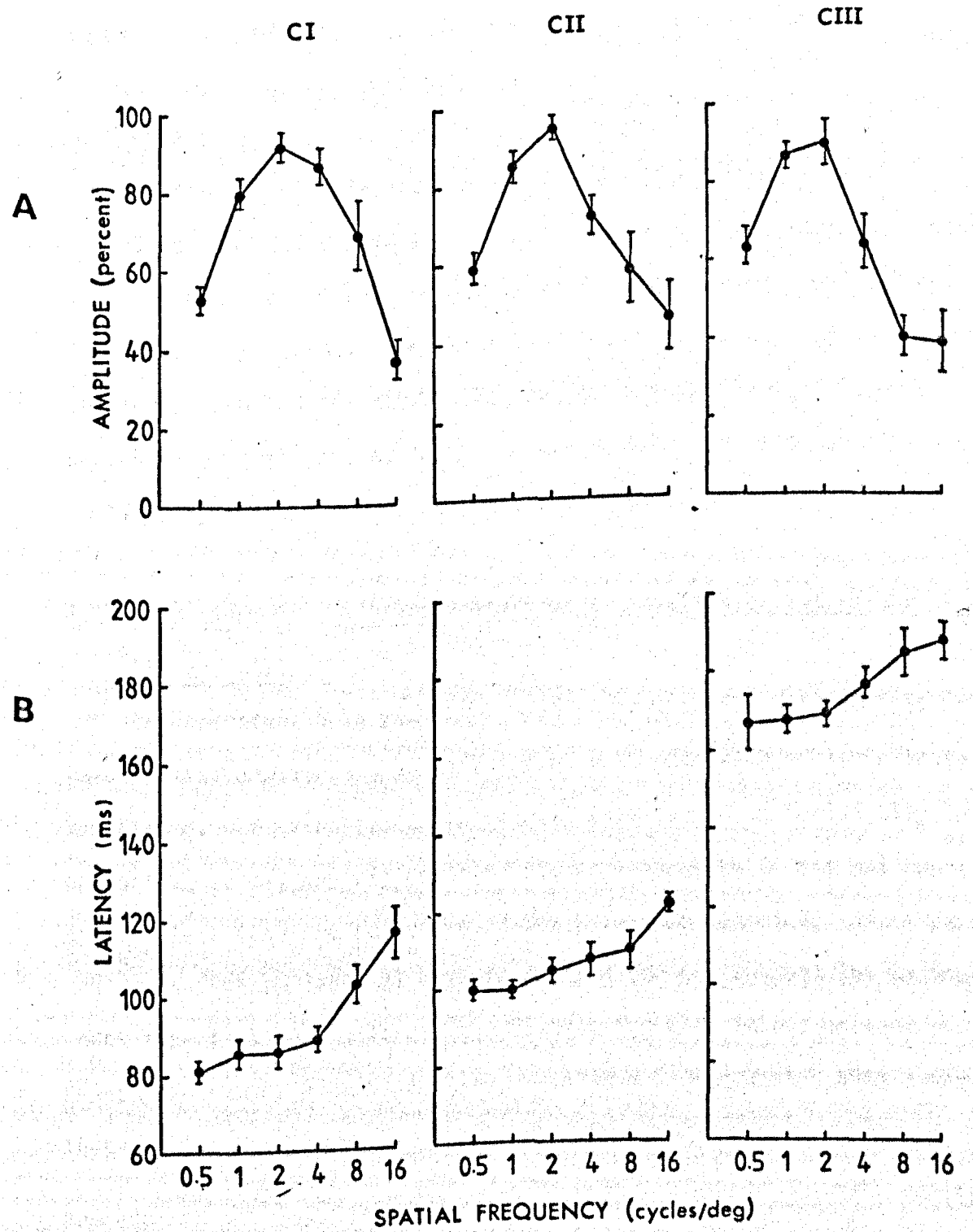

5μV
100ms
A
CI
B
CIII
CII
0.5
2.0
16.0
SPATIAL FREQUENCY (cycles/deg)

Fig. 15

Mean amplitude (a) and latency (b) of CI, CII and CIII as a function of the periodicity of a stimulus checkerboard.


CI
CII
CIII
A
AMPLITUDE (percent)
100
80
60
40
20
0
B
LATENCY (ms)
200
180
160
140
120
100
80
60
0.5 1 2 4 8 16
SPATIAL FREQUENCY (cycles/deg)

15a and 15b show the mean, normalized amplitude and mean latency respectively of each component as a function of periodicity (check size) for all six subjects. For all three components amplitude is maximal for a checkerboard of periodicity 2 cycles/deg (check width 15') and decreases with higher or lower periodicities, and latency increases as a function of periodicity, being shortest for the largest check size.

These results follow the trends reported by investigators of other types of pattern VEP (e.g. Rietveld et al., 1967; Parker and Salzen, 1977a,b). The optimal check size for eliciting CI, CII and CIII is within the range reported for other VEPs, and is somewhat larger (lower periodicity) than most estimates of the peak of the psychophysical contrast sensitivity function (e.g. Campbell and Robson, 1968).

4.3 Experiment 6: Detailed comparison of the size sensitivities of CI, CII and CIII

In Experiment 5 it was shown that components CI, CII and CIII all have maximal amplitude when elicited by a checkerboard of periodicity 2 cycles/deg. However, since the stimuli used varied in periodicity in one octave steps, any differences between components in optimal check size of less than one octave would not have been detected. Since Jeffreys and James (unpublished) have found that for one subject the optimal check size is slightly larger for CI than for CII, it was decided to repeat Experiment 5 using smaller variations in check size over a narrower range.

Procedure

Six subjects withnormal or corrected acuity were used. The procedure was the same as for Experiment 5 except that seven checkerboards were used, varying in periodicity from 1.0 cycles/deg to 4.0 cycles/deg in

steps of one third of an octave. Latencies were not recorded.

Results and Discussion

Fig. 16 shows the mean amplitude of each component as a function of checkerboard periodicity. As in the previous experiment, the maximum amplitude occurs at 2.0 cycles/deg for all three components. The preliminary finding of Jeffreys and James of a difference in the size sensitivities of CI and CII in one subject does not therefore appear to be general.

4.4 Experiment 7: The specificity of CI, CII and CIII to the size of an adapting pattern

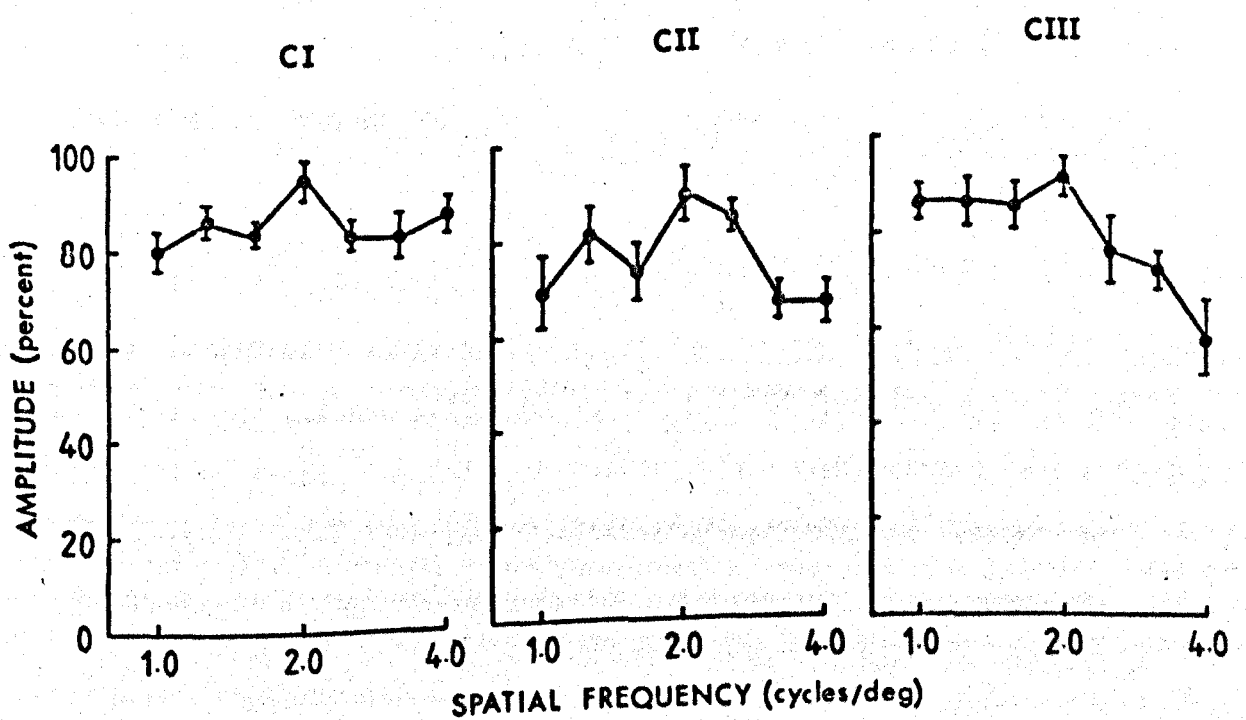
In this experiment the adaptation procedure described in section 2.1 was used to study the size-specificity of attenuation of CI, CII and CIII. Musso and Harter (1975) have studied transient VEPs in forward and backward masking paradigms using two brief patterned flashes separated by 40ms. They report variation in the amplitude of the response to the combined stimulus at latencies corresponding roughly to CII and CIII, but not CI, as a function of the sizes of the checkerboards forming the two stimuli.

Procedure

Six subjects with normal or corrected acuity were used. The stimuli were presented binocularly in tachistoscope A. For the study of CI, the test stimulus was either a vertical grating or a checkerboard of periodicity 2.0 cycles/deg. The grating stimulus was employed to allow direct comparison with psychophysical spatial frequency tuning functions; the checkerboard was used because it is a more effective stimulus for eliciting CI (see Fig. 8), while its size can be equally simply quantified in terms of its periodicity. The adaptation pattern was also

Fig. 16

Mean amplitude of CI, CII and CIII as a function of the periodicity of a stimulus checkerboard.


CI
CII
CIII
100
80
60
40
20
0
AMPLITUDE (percent)
1·0
2·0
4·0
SPATIAL FREQUENCY (cycles/deg)

either a vertical grating or a checkerboard. A range of seven adapting periodicities was used spanning three octaves in half-octave steps and centring on the test pattern size. VEPs were recorded under all four factorial combinations of grating and checkerboard adaptation and test patterns. For the study of CII and CIII, which cannot reliably be elicited by grating stimuli, the test pattern was always a checkerboard. The same test pattern size and the same range of adapting patterns was used as for the study of CI. The order of presentation of adaptation patterns was randomized.

Results

The effect of the size of a checkerboard on the VEP waveform elicited by a checkerboard is illustrated for one subject in Fig. 17a for CI and Fig. 17b for CII and CIII. Figs. 18a and 18b show the mean CI amplitude for all subjects elicited by a grating and a checkerboard test stimulus respectively as a function of adaptation periodicity. Values for checkerboard and grating adaptation patterns are shown separately. The curves for all four adaptation/test stimulus combinations show size tuning. CI amplitude is greatly attenuated when the adaptation pattern has the same periodicity as the test pattern but is progressively less attenuated by pre-exposure to increasingly larger or smaller stimuli. In the case of the checkerboard test pattern CI is less attenuated by pre-exposure to gratings than to checkerboards ($F(1,70)=13.9$, $p<.001$), whereas the grating test pattern data show no such difference ($F(1,70)=0.76$, $p>.05$). Figs. 18c and 18d show the mean CII and CIII amplitude respectively for all subjects as a function of the periodicity of the adaptation pattern for both grating and checkerboard adaptation. CII shows marked size tuning with a checkerboard test pattern, its

Fig. 17

VEP waveforms illustrating the effect of the size of an adapting checkerboard on the amplitude of (a) CI and (b) CII and CIII elicited by a checkerboard of periodicity 2.0 cycles/deg. Subject RL.

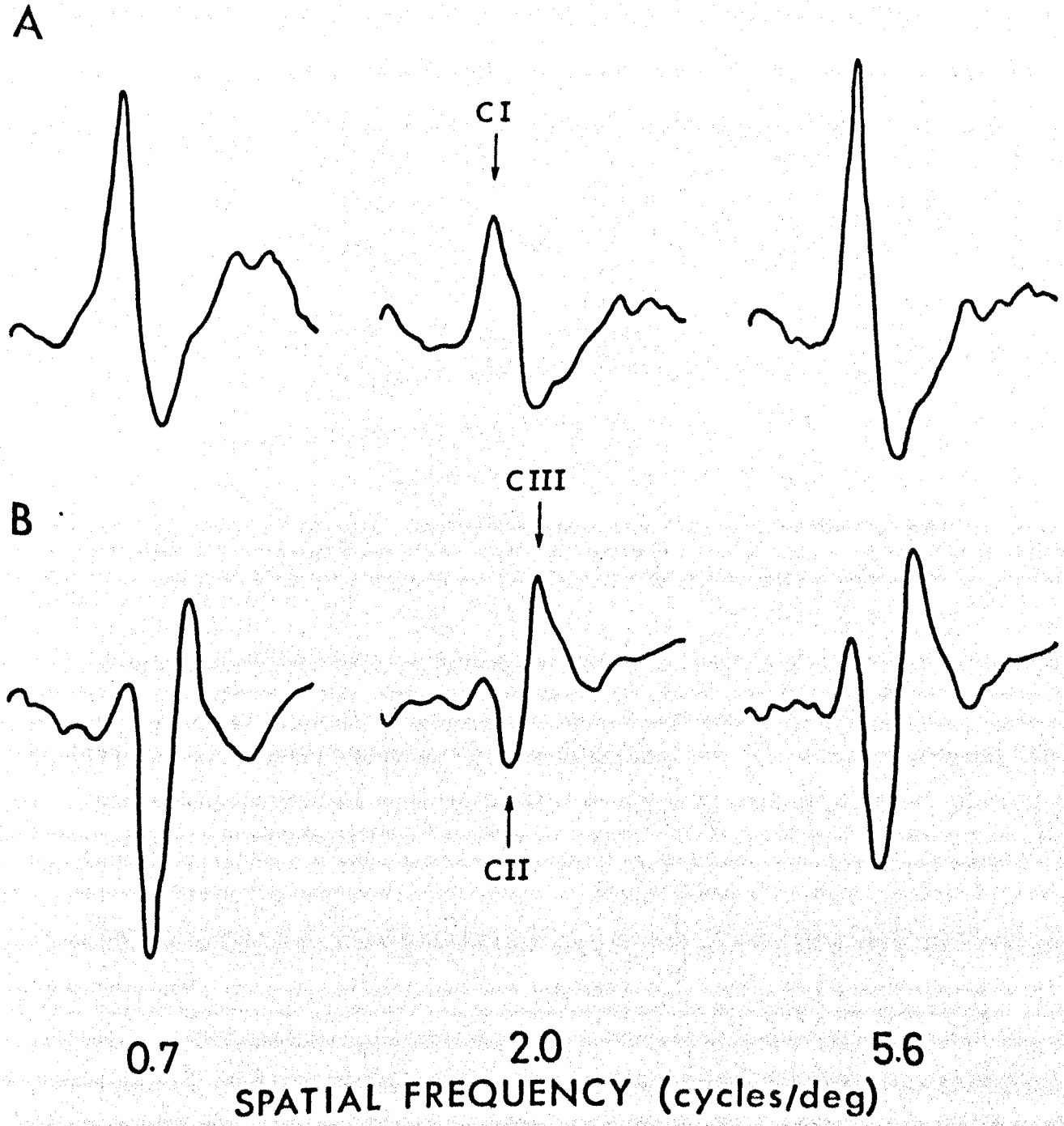
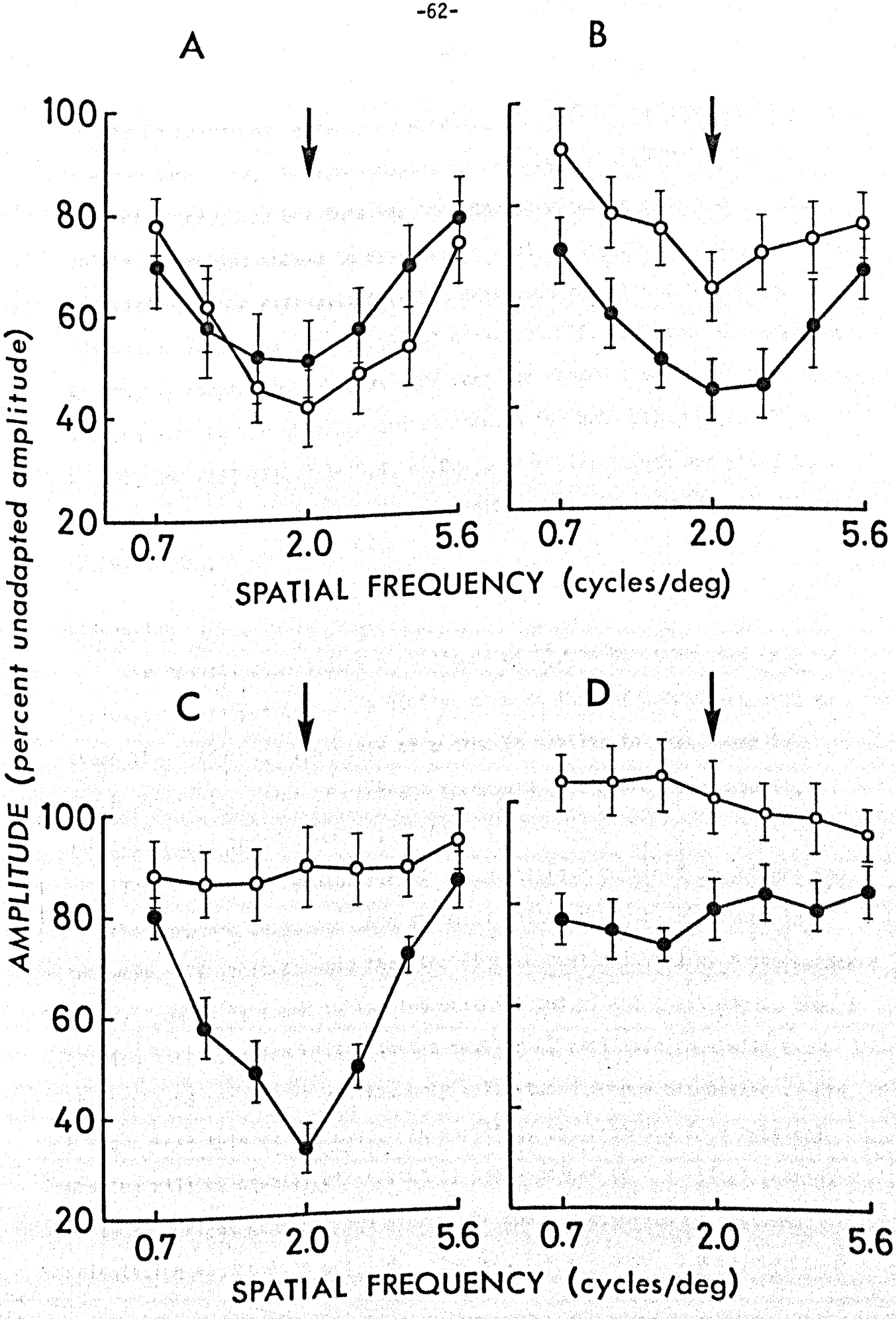

A
CI
B
CIII
CII
0.7
2.0
5.6
SPATIAL FREQUENCY (cycles/deg)

Fig. 18

Mean amplitude of (a) CI elicited by a grating, (b) CI elicited by a checkerboard, (c) CII elicited by a checkerboard and (d) CIII elicited by a checkerboard, as a function of the size of an adaptation grating (hollow circles) or checkerboard (solid circles). The size of the stimulus pattern (2.0 cycles/deg) is marked by an arrow in each case.


A
B
C
D
100
80
60
40
20
0.7
2.0
5.6
AMPLITUDE (percent unadapted amplitude)
SPATIAL FREQUENCY (cycles/deg)

amplitude being most attenuated when the adaptation and test checkerboards are the same size. Grating adaptation resulted in a small degree (about 12%) of attenuation but this was independent of adaptation size. CIII on the other hand showed no evidence of size tuning even for checkerboard adaptation. Some attenuation (about 22%) occurred with checkerboard adaptation which was independent of size, but CIII amplitude was unaffected by grating adaptation. Analysis of variance showed significant differences between grating and checkerboard adaptation for both CII ($F(1,70)=41.6$, $p<.001$) and CIII ($F(1,70)=18.4$, $p<.001$). For CII, though not CIII, the interaction between size and adaptation type was also significant ($F(6,70)=2.25$, $p<.05$).

Discussion

The results show that the amplitude of CI can be attenuated only by pre-exposure to patterns of a similar size to that of the pattern used to evoke the response. The width of tuning is similar to that found in psychophysical studies of contrast threshold (Blakemore and Campbell, 1969; Campbell and Kulikowski, 1966).

The pattern of results for CI under the four combinations of grating and checkerboard adaptation and stimulus patterns can be explained in two ways. If it is assumed that the CI component elicited by a checkerboard arises from cells tuned to the two orientations of the check edges, then a grating test stimulus will elicit a smaller CI amplitude than will a checkerboard because it excites only cells tuned to one orientation. Fig. 8 shows that this is the case. In addition, the response to a vertical grating will be equally attenuated by pre-exposure to a vertical grating or to an upright checkerboard since both contain elements of the same orientation as the test grating. However, the response to a checkerboard

will be more attenuated by pre-exposure to a similar checkerboard, which contains elements of both the orientations in the test pattern, than to a grating, which contains only one of these orientations and consequently will suppress only half the cells giving rise to the VEP. Figs. 18a and 18b show that this is the case.

However, in the light of the outcome of Experiment 8 (section 4.5), in which it is shown that more attenuation of CI occurs at the orientations of the fundamental Fourier components of the adaptation pattern than of the edges contained in the pattern, the assumption that the response to a checkerboard arises in cells tuned to the orientations of the check edges may not be valid. An alternative explanation of the present results is that the greater amplitude elicited by a grating pattern following grating adaptation than following checkerboard adaptation (Fig. 18a), which is a non-significant trend, reflects a real difference of the type found with a checkerboard test pattern (Fig. 18b). This difference can be attributed in both cases to the difference between the orientation of the grating and that of the fundamental Fourier component of the checkerboard.

In the case of CII and CIII, the results show that the sources of CII, but not those of CIII, are selectively sensitive to the size of the elements comprising the stimulus pattern. Jeffreys (1977) has suggested that CII originates in an area of prestriate cortex which is specialized for processing local contour or form, while CIII originates in a separate area of prestriate cortex of as yet unknown specialization. This notion of specialization is consistent with Zeki's (e.g. 1978a) findings that monkey prestriate cortex is subdivided into several anatomically and functionally distinct regions, each of which deals primarily with a different aspect of the visual stimulus (depth, colour, motion, etc.) and each of which probably receives direct input from the less specialized striate cortex.

The finding that CII is size sensitive would be expected if it reflects the processing of local contour information, and the finding that attenuation of CIII is independent of size suggests that CIII reflects the processing of some other attribute of the stimulus. The almost complete lack of attenuation of CII and CIII following grating adaptation reflects the relative insensitivity of either to grating test stimuli. Jeffreys (1977), however, reports that adaptation to a suitable pattern can result in more marked attenuation of CIII than is shown here.

It seems likely that the variance at 110ms reported by Musso and Harter (1975) corresponds to the variation in CII amplitude reported here for checkerboard adaptation, although at the latencies of CI and CIII no such correspondence exists.

The results of Experiment 7 provide VEP evidence consistent with the existence in striate cortex and in one region of prestriate cortex of size-sensitive cells of the type which have been found in monkey striate cortex (e.g. Campbell, Cooper and Enroth-Cugell, 1969).

4.5 Experiment 8: The role of the fundamental Fourier component of an adapting pattern in the attenuation of CI.

The aim of this experiment was to determine whether amplitude attenuation of CI, which was shown in Experiment 1 to be orientation-specific, is specific to the orientations of the fundamental Fourier components of the adaptation pattern or to the orientations of the edges contained in the pattern. Since the experiment necessitated the use of grating stimuli, CII and CIII were not studied.

Procedure

Six subjects with normal acuity were used. The stimuli were presented binocularly in tachistoscope A. In the first part of the experiment the stimulus pattern was a horizontally oriented square-wave grating. Gratings

of three spatial frequencies (0.7, 2.0 and 5.6 cycles/deg) were used in separate conditions. In the case of the 2.0 cycles/deg grating, the adaptation pattern was either a checkerboard with vertical and horizontal check edges and a check width equal to the bar width of the grating (15'), or an obliquely oriented checkerboard of an increased check size (21') such that the diagonal of each check subtended 30'. The fundamental Fourier components of the latter checkerboard lie at 2.0 cycles/deg in the vertical and horizontal directions. In the case of the other two stimulus gratings, the sizes of the adaptation patterns were adjusted to the same proportions. In the second part of the experiment the stimulus pattern was a checkerboard with vertical and horizontal check sides. The adaptation pattern in this case was a square-wave grating, either horizontally orientated and with the same bar width as the test pattern check width, or obliquely orientated and with the spatial frequency of the fundamental Fourier component of the test checkerboard, that is a factor of 1.4 above the spatial frequency of the horizontal adaptation grating. Again this procedure was repeated with three different test sizes and corresponding adaptation sizes.

Results

The VEP waveforms elicited by a horizontal grating stimulus without adaptation and following adaptation to horizontal and oblique checkerboards are illustrated for one subject in Fig. 19. Figs. 20a and 20b show the mean CI amplitude elicited by a horizontal grating and checkerboard respectively for all subjects under horizontal and oblique adaptation conditions, as a function of periodicity. In all cases, both adaptation patterns cause considerable amplitude attenuation but the effect is more marked in the case of oblique adaptation. Analysis of variance shows that

Fig. 19

VEP waveforms showing the amplitude of CI elicited by a horizontal grating stimulus, (a) in the absence of an adaptation stimulus, (b) after adaptation to a horizontally oriented checkerboard pattern, and (c) after adaptation to an obliquely oriented checkerboard. Subject VW.

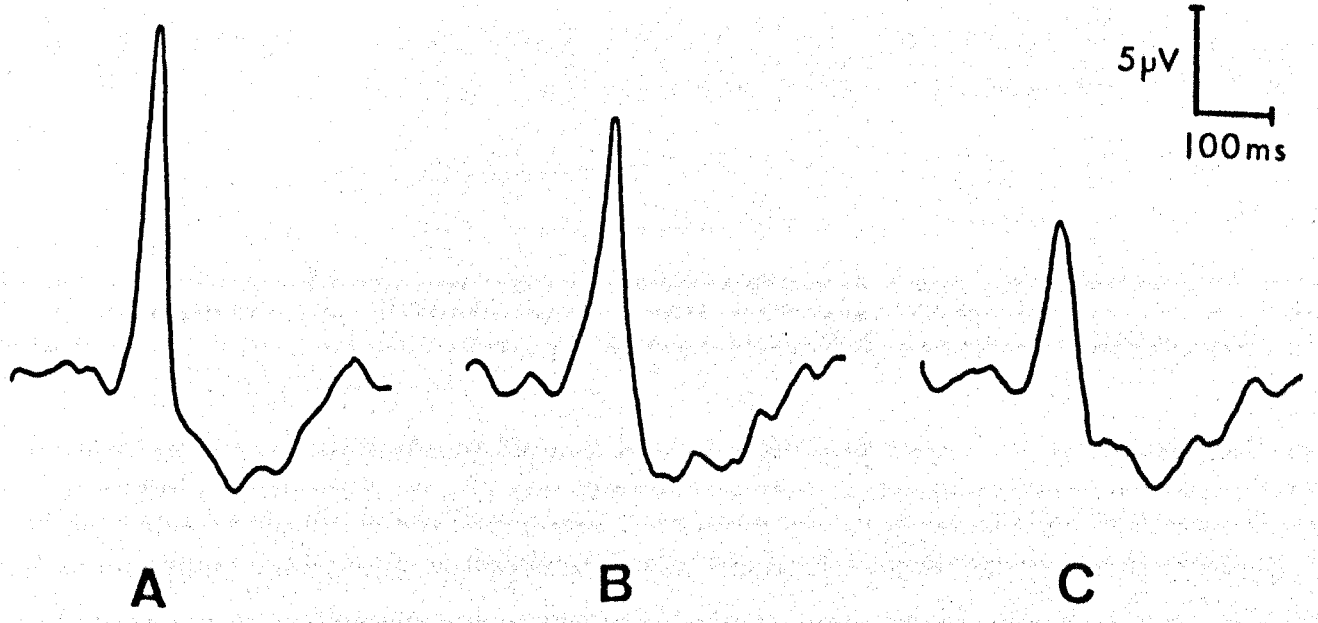
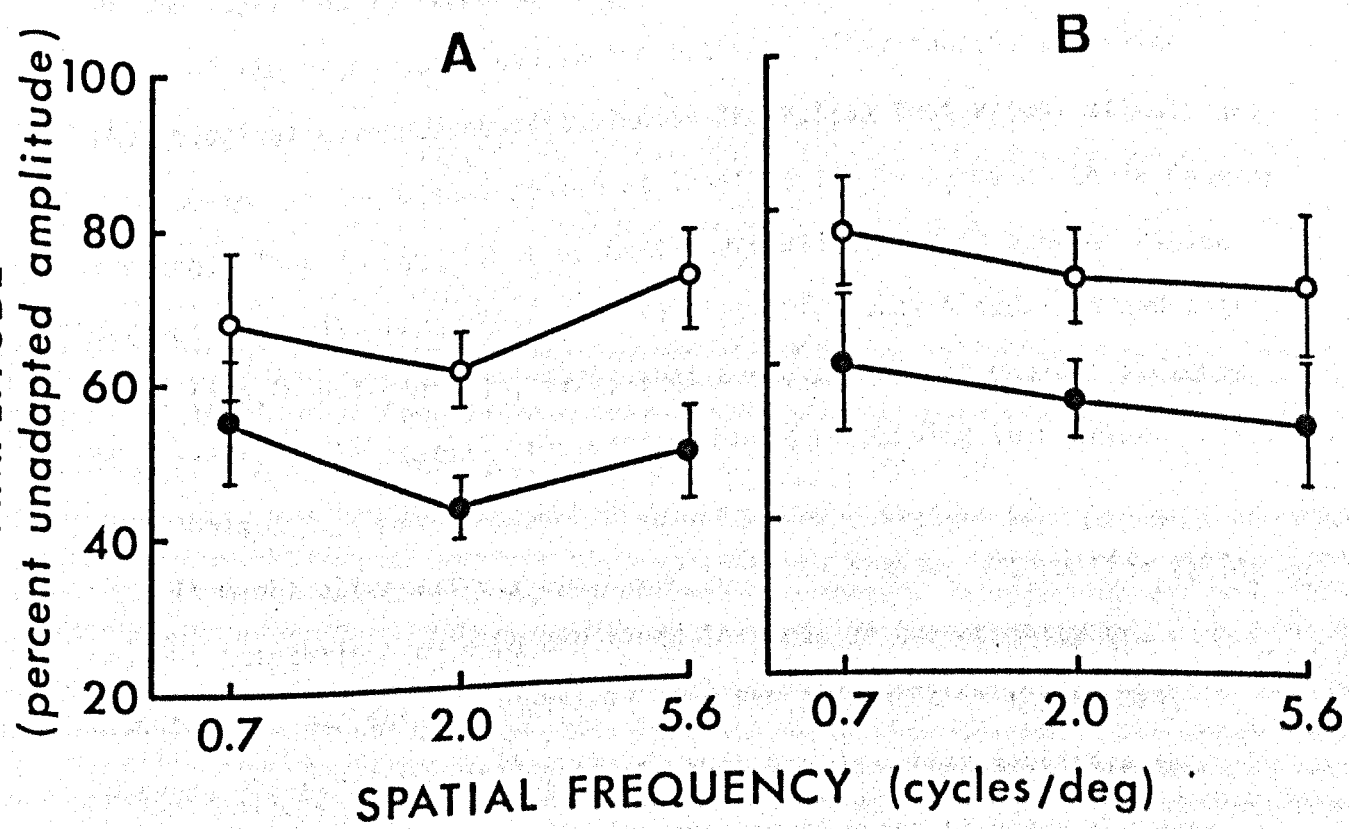

5μV
100ms
A
B
C

Fig. 20

Mean CI amplitude elicited by (a) a horizontal grating stimulus of the size shown following adaptation to a horizontally oriented checkerboard (hollow circles) or an obliquely oriented checkerboard (solid circles) of appropriate size, and (b) a checkerboard of the size shown following adaptation to a horizontal grating (hollow circles) or an oblique grating (solid circles) of appropriate size.


A
B
AMPLITUDE
(percent unadapted amplitude)
100
80
60
40
20
0.7
2.0
5.6
0.7
2.0
5.6
SPATIAL FREQUENCY (cycles/deg)

amplitude varies significantly as a function of adaptation type (horizontal or oblique) for both grating test stimuli ($F(1,30)=6.13$, $p<.05$) and checkerboard test stimuli ($F(1,3)=5.21$, $p<.05$).

Discussion

These results show that at the level of the source of CI (thought to be in striate cortex) greater adaptation occurs at the orientations of the major Fourier components present in an adaptation pattern than at those of the edges contained in the pattern. They therefore provide physiological evidence consistent with the notion that visual stimuli are represented in the visual system at least partly in terms of their Fourier spectra. They do not, however, constitute evidence that spatial vision derives primarily from a Fourier transform of visual space. Indeed data exist (e.g. Henning et al., 1975) that are difficult to explain in terms of narrowly tuned spatial frequency channels responding to Fourier components.

It might alternatively be argued that the greater attenuation following oblique adaptation could be explained in terms of the activity of hypothetical bar detectors aligned with the diagonals of the checks. However, the receptive fields of any such bar detectors sensitive to vertical and horizontal bars would cover equal areas of black and white and so would not be activated. There would therefore be no adaptation at vertical and horizontal orientations; in fact CI amplitude is considerably attenuated in this situation (Fig. 20, hollow circles). The results are better explained in terms of the existence of spatial frequency or size channels which respond not only to Fourier components but also to periodicities. Many patterns, including checkerboards, have a complex Fourier spectrum but have a simple periodicity. It is possible that spatial frequency channels are sensitive to such periodicities, so

that adaptation occurs both at the orientations of the prominent Fourier components and at the orientations of the periodicity of the checks. The adaptation resulting from exposure to a compound grating of the type used by Henning et al. (1975) (see section 4.1) is also explicable in this way, since such a grating has a periodicity at a much lower frequency than the lowest Fourier component.

4.6 Experiment 9: Interocular transfer of size-specific attenuation of CI and CII.

In Experiment 7 it was found that size-specific attenuation of CI and CII occurs following adaptation. In this experiment interocular transfer of this attenuation is measured in order to determine whether the effect is central or peripheral in origin.

Procedure

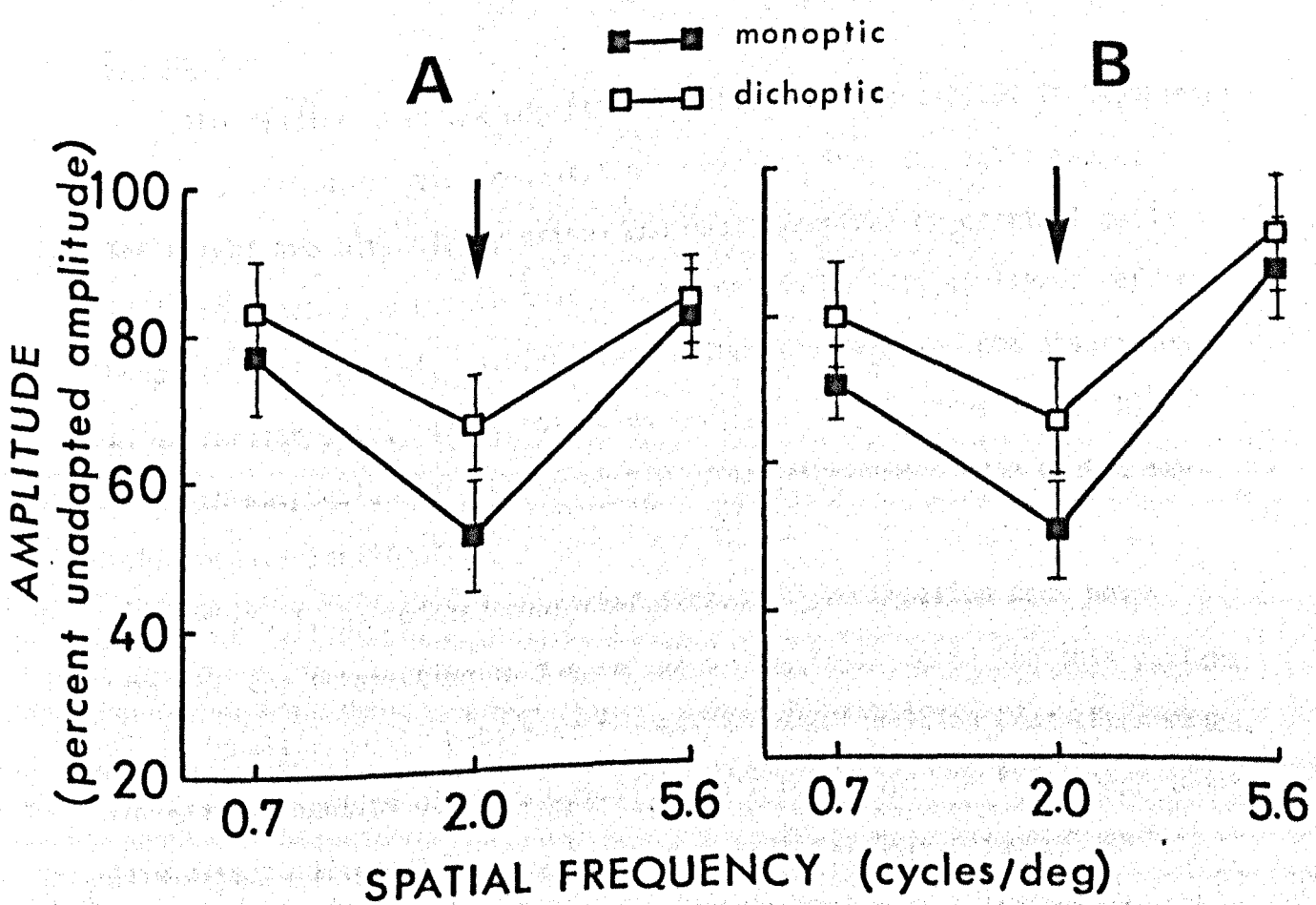
Six subjects with normal or corrected acuity and normal stereoacuity were used. Although tachistoscope B would have been better suited, tachistoscope A was used since the experiment was conducted before tachistoscope B had been constructed. Polarizing filters were used to present the test stimulus to the right eye and the adapting stimulus to either the right eye (monoptic condition) or the left eye (dichoptic condition). A range of three periodicities was used, again spanning three octaves centred on the test periodicity (2.0 cycles/deg). Both adaptation and test patterns were checkerboards. Because of the presence of polarizing filters the mean luminance was reduced from the usual 216 cd m^{-2} to 61 cd m^{-2}.

Results

The mean CI and CII amplitudes are shown in Figs. 21a and 21b

Fig. 21

Mean CI (a) and CII (b) amplitude elicited by a checkerboard stimulus pattern as a function of the periodicity of an adaptation checkerboard presented monoptically (solid square) and dichoptically (hollow squares). The size of the stimulus pattern is shown by an arrow in each case.


monoptic
dichoptic
A
B
AMPLITUDE
(percent unadapted amplitude)
100
80
60
40
20
0.7
2.0
5.6
0.7
2.0
5.6
SPATIAL FREQUENCY (cycles/deg)

respectively for both monoptic and dichoptic conditions, as a function of adaptation check size. Both CI and CII show size selectivity in the dichoptic as well as the monoptic condition, amplitude attenuation being greater when the adaptation and test checkerboards are the same size than when they differ.

Discussion

The finding that the amplitude attenuation demonstrated in Experiment 7 occurs with dichoptic presentation indicates that the cells mediating the effect are binocularly driven and must therefore be cortical cells. It is reasonable to assume that the attenuation of CI, at least, reflects adaptation of the cells giving rise to the component and not adaptation at an earlier site. It is possible, however, that attenuation of CII reflects adaptation in striate cortex, from which the source of CII may well receive its input.

It should be pointed out that dichoptic presentation does not preclude the interaction in the cortex of the response to the test pattern with signals from the retina of the adapted eye resulting from afterimages. The steady fixation of the adaptation pattern employed in these experiments gave rise to afterimages, which although weak may have affected VEP amplitude. Smith (1977) has shown that afterimages do contribute to threshold elevation in spatial frequency adaptation and a similar contribution to VEP amplitude is possible. However, the reported effects of afterimages are small and it seems probable that the effects reported in the present study are essentially cortical in origin.

4.7 Experiment 10: Comparison of the degree of interocular transfer of attenuation of CI and CII

In Experiment 9 it was shown that attenuation of CI and CII following

adaptation transfers interocularly. Unfortunately the use of polarizing filters in conjunction with half-silvered mirrors was not totally effective in separating the images presented to the two eyes, and may also have given rise to small luminance differences between fields. It was therefore not possible to draw reliable quantitative conclusions concerning the proportion of interocular transfer of attenuation of the components studied and so to make quantitative statements concerning the degree of binocularity of their sources (see section 4.1). Experiment 10 consists of a more precise measurement of the degree of interocular transfer of the attenuation of CI and CII which occurs following adaptation.

Procedure

Six subjects with normal or corrected acuity and normal stereoacuity were used. The stimuli were presented in tachistoscope B. The test pattern and blank field were presented in the two fields which were presented to the right eye only, and the adaptation pattern was presented in the field which could be presented to either eye by means of a shutter. This ensured that the luminances of the patterns did not vary between viewing conditions. The adaptation and test patterns were both checkerboards of periodicity 2.0 cycles/deg (15' checks). The same two viewing conditions (monoptic and dichoptic) were used as in Experiment 9.

Results

Fig. 22 shows for one subject the VEP waveforms elicited by a checkerboard without adaptation and following monoptic and dichoptic adaptation to a similar checkerboard. The mean amplitudes for all six subjects under monoptic and dichoptic viewing conditions are shown in Figs. 23a and 23b for CI and CII respectively. Both monoptic and dichoptic

Fig. 22

VEP waveforms showing the amplitudes of CI (a) and CII (b) elicited by a checkerboard stimulus without adaptation, following monoptic adaptation to a similar checkerboard and following dichoptic adaptation. Subject IEB.

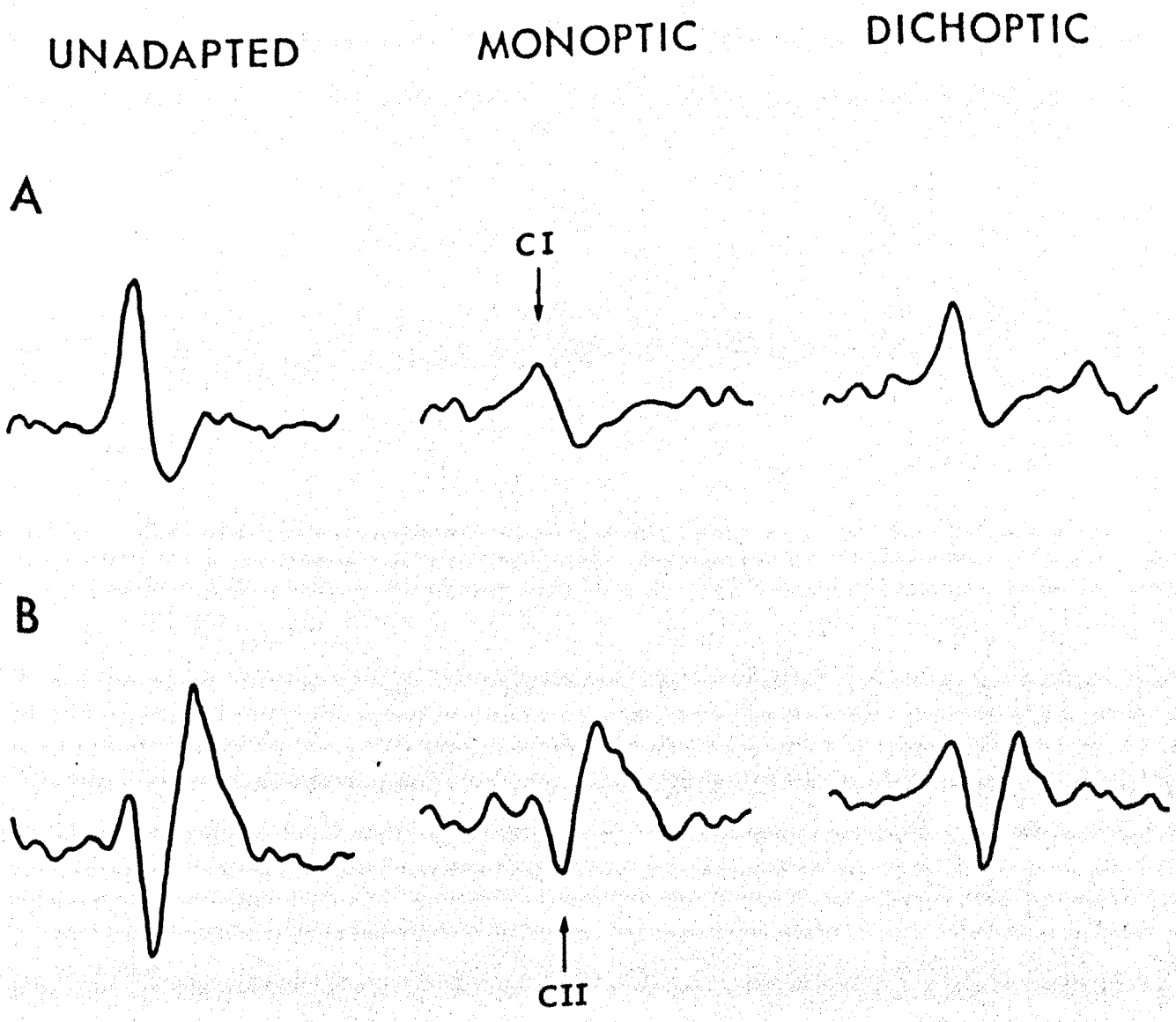
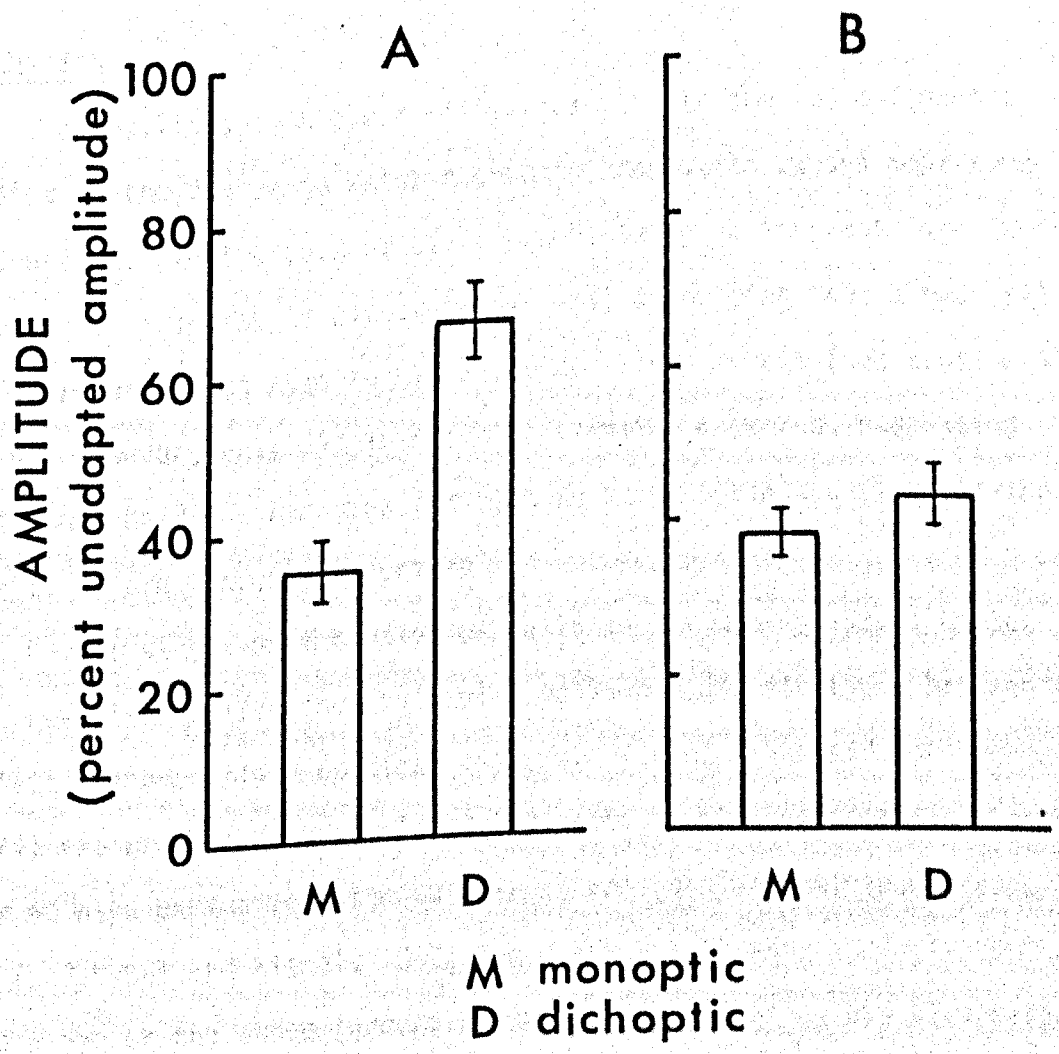

UNADAPTED
MONOPTIC
DICHOPTIC
A
CI
B
CII

Fig. 23

Mean CI (a) and CII (b) amplitude elicited by a checkerboard stimulus following monoptic and dichoptic adaptation to a similar checkerboard.


A
B
AMPLITUDE
(percent unadapted amplitude)
100
80
60
40
20
0
M
D
M
D
M monoptic
D dichoptic

adaptation cause attenuation of the amplitude of CI, but significantly greater attenuation occurs with monoptic adaptation ($F(1,10)=25.6$, $p<.001$). In the case of CII monoptic and dichoptic adaptation result in a similar degree of amplitude attenuation ($F(1,10)=2.29$, $p>.05$). The proportion of interocular transfer of attenuation (i.e. the ratio of dichoptic to monoptic attenuation) is 51% for CI and 92% for CII.

Discussion

The results show a clear difference between the two components studied in the degree to which dichoptic adaptation causes amplitude attenuation. In the case of CII (thought to arise in prestriate cortex) interocular transfer is almost total (92%) suggesting that almost all the neurones giving rise to CII are binocularly driven (see section 4.1). For CI, however, only 51% interocular transfer occurred, suggesting that about half the neurones (thought to be in striate cortex) giving rise to CI are monocularly driven.

Recent single-unit studies of cells in the monkey visual cortex have revealed a difference in ocular dominance distributions between the striate and prestriate cortical regions. Baker, Grigg and von Noorden (1974) report that of a sample of 178 units in macaque prestriate cortex only 4% were exclusively monocularly driven (ocular dominance groups 1 and 7 of Hubel and Wiesel, 1962) and a further 8% were strongly dominated by one eye or the other (groups 2 and 6). Zeki (1978b) has also recently reported that of a very large sample (1500) of units in various sub-regions of prestriate cortex, the great majority were binocularly driven. In striate cortex, on the other hand, about half the units encountered by Baker et al. were strongly or completely dominated by one eye (groups 1, 2, 6 and 7) including 23% which were exclusively monocularly driven.

Schiller, Finlay and Volman (1976) found a similar proportion of binocularly driven cells in striate cortex (72% of units fell in groups 2-6, the remainder were monocularly driven), while Poggio (1972) has reported that as few as 26% of foveal and parafoveal striate cells are binocular (groups 3-5). It seems clear, therefore, that monocularly driven units are considerably more common in striate cortex than in prestriate cortex of the monkey.

The result of this experiment suggests that the same difference in binocularity between striate and prestriate regions is found in man. However, although it is thought that CI arises in striate cortex and CII in prestriate cortex (Jeffreys, 1971), it cannot be assumed that these components reflect the activity of all classes of cell within these areas. Firstly, Zeki (e.g. 1978a) has found that monkey prestriate cortex can be subdivided into a number of anatomically and functionally distinct regions, and it is likely that human prestriate cortex is similarly divided. Jeffreys (1977) has suggested that CII originates only in one such region. However Zeki (1978b) reports no differences in binocularity between regions, and so the binocularity of CII is probably typical of all prestriate regions. Secondly, as a result of the use of a small, centrally fixated field in the present experiment, the components measured reflect the activity of the foveal and parafoveal cortical representations only. In fact Jeffreys and Axford (1972) have found that CI originates mainly in the parafoveal region, and CII mainly in the foveal region. Albus (1975) has found that in cat striate cortex the proportion of binocularly driven cells increases with retinal eccentricity from 35% in the fovea to 74% at 6-12 deg. If such a relationship pertains in man, then the degree of interocular transfer of attenuation of CI and CII must be interpreted in the light of knowledge

of the eccentricities of their origins. However, since CI originates more eccentrically than CII but shows less interocular transfer, the difference in interocular transfer reported here cannot be explained in terms of the difference in eccentricity of the origins of the two components.

It is therefore concluded that in man almost all foveal neurones in at least one region of prestriate cortex are binocular, while about half of all parafoveal striate neurones are monocular.

CHAPTER FIVE

COLOUR SPECIFICITY

5.1 Introduction

Retinal ganglion cells receive input from one or more of three cone types, containing pigments sensitive to red, green and blue light respectively. Most monkey retinal ganglion cells show opponent colour properties (Gouras, 1968), receiving antagonistic signals from different cone mechanisms so that they are excited by certain wavelengths and inhibited by others. Opponent-colour cells also predominate in the monkey lateral geniculate nucleus (De Valois, 1965; Wiesel and Hubel, 1966), and must therefore provide a major afferent input to the striate cortex. Opponent-colour cells have been observed in monkey striate cortex; however they appear to be much less numerous than at earlier stages (e.g. Hubel and Wiesel, 1968; Dow, 1974; Gouras, 1974). In prestriate cortex, although one anatomical region contains predominantly colour-coded cells (Zeki, 1973), in all other regions such cells are rare (Zeki, 1974).

A number of psychophysical studies have implicated the existence of colour-coded cells in the human visual cortex. McCollough (1965) found that following alternate adaptation to orange vertical and blue horizontal lines, a test grating presented in white light appears blue when vertical and orange when horizontal. She attributed this orientation-contingent colour aftereffect to adaptation of cortical cells whose sensitivity is restricted not only to a narrow range of orientations but also to a narrow range of wavelengths. A corresponding colour-contingent tilt aftereffect has also been reported. Held and Shattuck (1971) found that after subjects alternately viewed red stripes tilted clockwise from vertical and green stripes tilted equally but anticlockwise, vertical test stripes appeared to be tilted anticlockwise when red and clockwise when green. This effect shows the same tuning function as the conventional tilt

aftereffect (Lovegrove and Over, 1973), and like the McCollough effect, it has been attributed to the adaptation of cortical cells selectively sensitive to both orientation and colour. (The neural fatigue explanation of McCollough and related effects has been questioned; see for example MacKay and MacKay (1974), Skowbo, Timney, Gentry and Marant (1975).) Colour sensitivity has also been demonstrated for the motion aftereffect (Hepler, 1968; Farreau, Emerson and Corballis, 1972) and the size aftereffect (Lovegrove and Over, 1972; Breitmeyer and Cooper, 1972).

With dichoptic presentation of adaptation and test stimuli, colour specificity of all three aftereffects is lost. Indeed, Stromeyer (1972) has demonstrated that opposite McCollough effects can be simultaneously induced in the two eyes. This suggests that cortical cells which are tuned to both orientation and colour have largely monocular inputs, a suggestion which has recently been confirmed by Michael (1978a,b), who found that most opponent-colour cells encountered in monkey striate cortex were exclusively monocularly driven. The only binocularly driven colour sensitive units encountered by Michael were a small number of complex cells which could be excited only by moving stimuli (Michael, 1978c).

Limited evoked potential evidence of colour specificity in human visual cortex also exists. Regan and Spekreijse (1974) have reported that VEPs can be elicited by the onset of a pattern of equiluminant red and green checks, and also by the phase-reversal of such a pattern. May, Leftwich and Aptaker (1974) have found that the VEP elicited by 9Hz phase reversal of a coloured grating is more attenuated following adaptation to a grating of the same colour than to one of the complimentary colour. In Experiment 11 of this thesis, the specificity of the amplitude attenuation of CI and CII to the colour of the adaptation and

test patterns is examined under both monoptic and dichoptic adaptation conditions. In Experiment 12 the colour specificity of the reversal VEP is studied in an attempt to reconcile the results of Experiment 11 with those of May et al. (1974).

5.2 Experiment 11: The specificity of CI and CII to the colour of an adapting pattern

In this experiment the specificity of amplitude attenuation of the VEP components CI and CII, elicited by a coloured checkerboard, to the colour of an adapting checkerboard is examined. In view of the failure of psychophysical colour specificity to transfer interocularly (see section 5.1) amplitude was measured under both monoptic and dichoptic adaptation conditions.

Procedure

Six subjects with normal acuity, normal colour vision and normal stereoacuity were used. The stimuli were presented in tachistoscope B. The test stimulus pattern was a checkerboard of periodicity 2 cycles/deg, and was viewed through a Wratten colour filter so that it appeared either red (filter 29) or green (filter 61). The adaptation stimulus was also a checkerboard viewed through either a red or a green filter. Three adaptation pattern sizes were used: 0.7, 2.0 and 5.6 cycles/deg. The test pattern was always presented to the subject's right eye; the adaptation pattern was presented via a single tachistoscope field either to the right eye (monoptic conditions) or the left eye (dichoptic conditions) using a shutter. This ensured that the luminance of the patterns did not vary between conditions. All four combinations of red and green adaptation and test patterns were used to produce two same-colour

conditions (R-R and G-G) and two different-colour conditions (R-G and G-R). VEPs were also recorded for each stimulus pattern in the absence of adaptation.

Results

The VEP waveforms elicited by a red checkerboard following monocular adaptation to a red and a green adaptation checkerboard of the same or a different size are illustrated for one subject in Fig. 24. Fig. 25 shows the mean CI and CII amplitudes for all subjects as a function of adaptation pattern size for all colour conditions under monoptic adaptation (Fig. 25a) and dichoptic adaptation (Fig. 25b). In all cases amplitude is considerable attenuated following adaptation to a checkerboard of the same size and relatively unaffected by adaptation to a pattern of a different size (see section 4.4), but is independent of whether the test and adaptation patterns are the same colour or are of complimentary colours.

Discussion

The results indicate that attenuation of neither CI nor CII is colour-specific, and hence that the cells contributing to these components are not colour coded. In the case of CI, this result is surprising in view of the evidence that a substantial minority of cells in monkey striate cortex show colour-opponent properties, particularly those receiving a direct input from the LGN (Michael, 1978a). The result is also inconsistent with the psychophysical studies reviewed in the preceding section which would lead to the expectation that CI and/or CII might show colour-specificity under monoptic but not dichoptic adaptation conditions. One possible explanation is that CI originates mainly in the superficial layers of the striate cortex, where most cells

Fig. 24

VEP waveforms illustrating the effect of the colour and size of an adaptation checkerboard on the amplitudes of CI (a) and CII (b) elicited by a red checkerboard. Subject ATS.

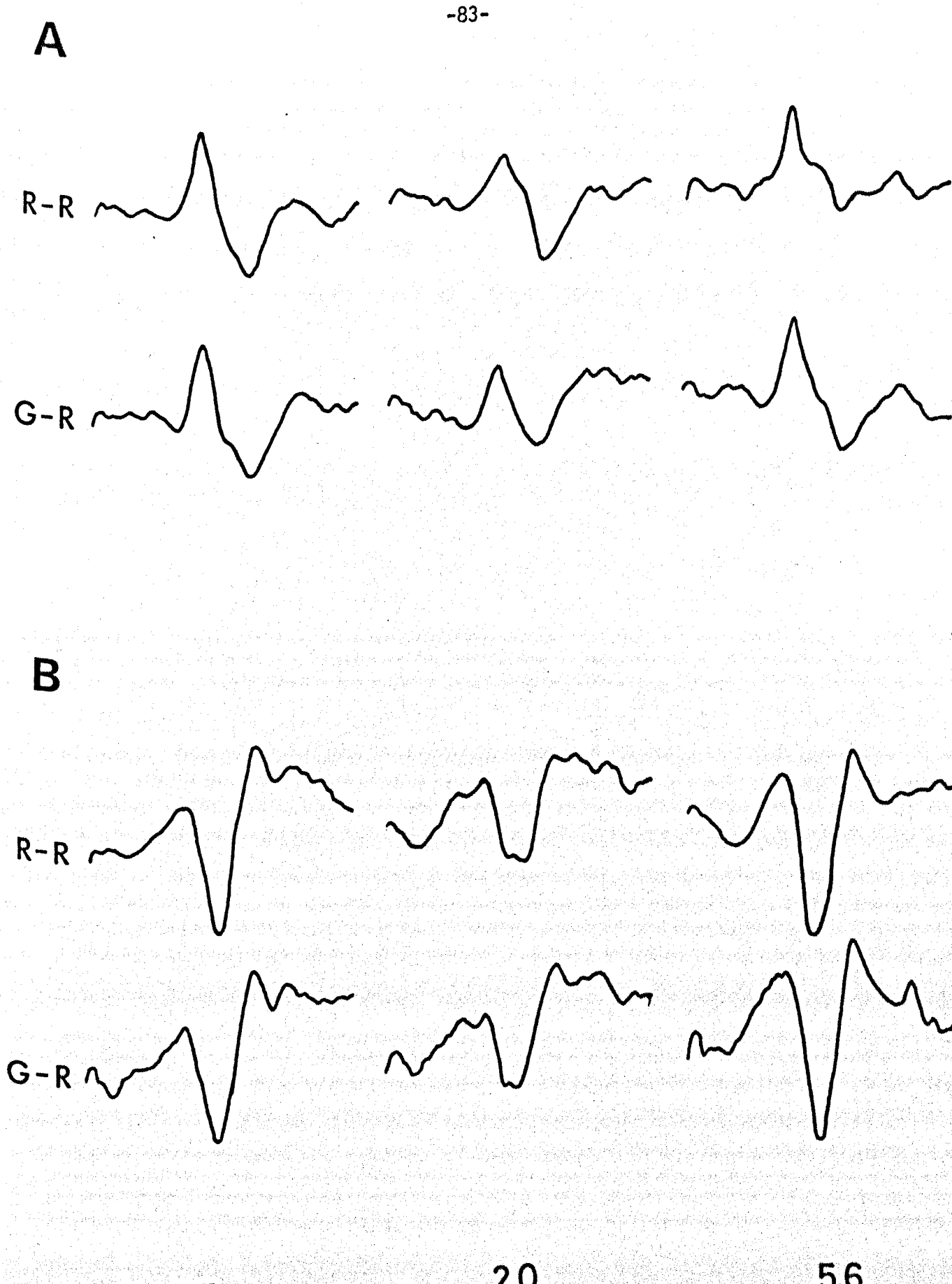
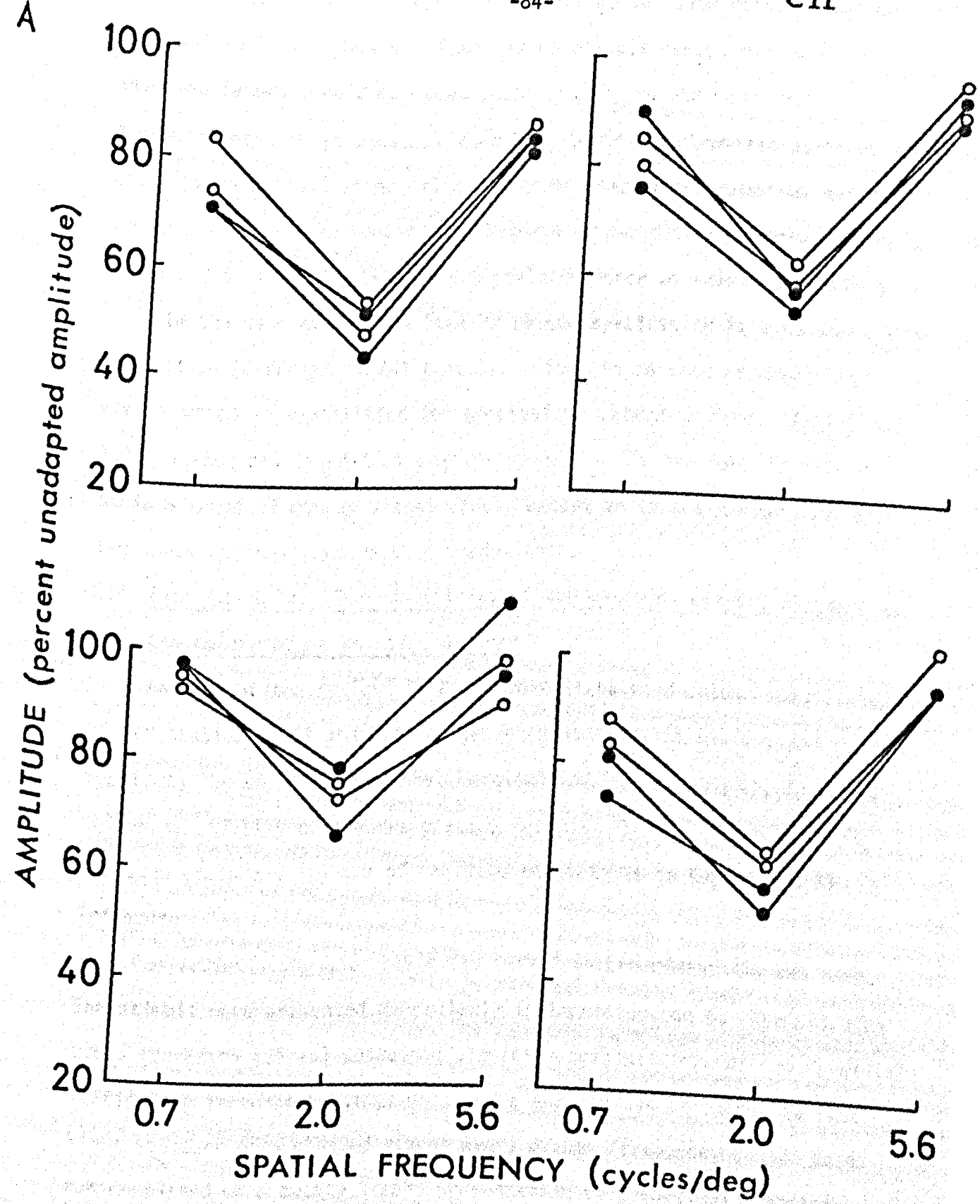

A
R-R
G-R
B
R-R
G-R
0.7
2.0
5.6
SPATIAL FREQUENCY (cycles/deg)

Fig. 25

Mean CI and CII amplitudes for the four combinations of red and green adaptation and stimulus checkerboards under monoptic (a) and dichoptic (b) adaptation.


A
100
80
60
40
20
AMPLITUDE (percent unadapted amplitude)
0.7
2.0
5.6
SPATIAL FREQUENCY (cycles/deg)
homochromatic
heterochromatic

that are responsive to stationary stimuli do not show colour opponency (Michael 1978a,b); however, there is no obvious reason why superficial and deep layers should not contribute equally to VEP components. Alternatively, it is possible that the use of monochromatic patterns does not provide optimal stimulation for opponent-colour mechanisms and that the use of a pattern containing elements of two different colours (see Regan and Spekreijse, 1974) might yield evidence of colour specificity.

In the case of CII the lack of colour specificity is consistent with the notion (Jeffreys, 1978) that CII arises in an area of prestriate cortex which is specialized for processing contour or form. Zeki (1973, 1974, 1978b) has found that colour-opponent cells are rare in all non-striate areas of monkey visual cortex except V4 (the anterior bank of the lunate sulcus), where they predominate.

5.3 Experiment 12: The specificity of the pattern-reversal response to the colour of an adapting pattern

In view of the failure in Experiment 11 to find colour specificity of attenuation of CI and CII following adaptation, it was decided to replicate the experiment of May, Leftwich and Aptaker (1974), in which colour specificity of the 9Hz grating reversal VEP was reported, using the same equipment and one of the same subjects as in Experiment 11.

Procedure

One subject, who had previously served in Experiment 11, was used. The stimuli were presented binocularly in tachistoscope A. The stimulus cycle (duration 125 ms) contained alternate presentations of two identical, vertical square-wave gratings which were 180 deg out of phase, so that light and dark bars changed places every 62.5ms (frequency 8Hz). Each run consisted of a twenty second presentation of a vertical adapting grating followed, after an interval of four seconds, by 40 cycles of the alternating test gratings. In order to avoid the build up of retinal afterimages, during the adaptation period the subject allowed his gaze to

wander over the pattern. The stimuli were viewed through Wratten colour filters so that the adaptation and test stimuli each appeared either red (filter 29) or green (filter 61). All four combinations of red and green adaptation and test stimuli were used. In order to test the possibility that any amplitude attenuation recorded might result from chromatic adaptation in the retina rather than adaptation in cortical, oriented cells, VEPs were also recorded following adaptation to a uniform field under the same four colour combination conditions. In addition, VEPs were recorded in the absence of adaptation for each test stimulus colour. The experiment was conducted using gratings of two spatial frequencies: 1.0 cycles/deg (as used by May et al., 1974) and 2.0 cycles/deg (used in Experiment 11). VEPs were recorded from an electrode positioned on the midline, 2.5cm above the inion, with reference to the right earlobe. In each condition four identical runs were conducted successively and the response to all 160 cycles of the test stimulus were averaged together. Amplitude measures of two types were obtained. May et al. measured the peak-to-trough amplitude N_2-P_2 (see Fig. 26); this was also done in the present experiment in order to facilitate comparison of the results with those of May et al.. However, in view of the "steady-state" conditions associated with 8Hz reversal responses (see section 1.1), it was considered more meaningful to measure overall amplitude variation, in the manner employed in Experiment 4 (section 3.5).

Results

Fig. 26 shows the VEP waveforms elicited by a green grating of 1.0 cycles/deg reversing in phase at 8Hz without adaptation, following adaptation to a uniform field, and following adaptation to a coloured

Fig. 26

VEP waveforms elicited by 8Hz phase reversal of a green grating (a) without adaptation, (b) following adaptation to a green or red uniform field, and (c) following adaptation to a green or red grating of the same orientation and size. Subject ATS.

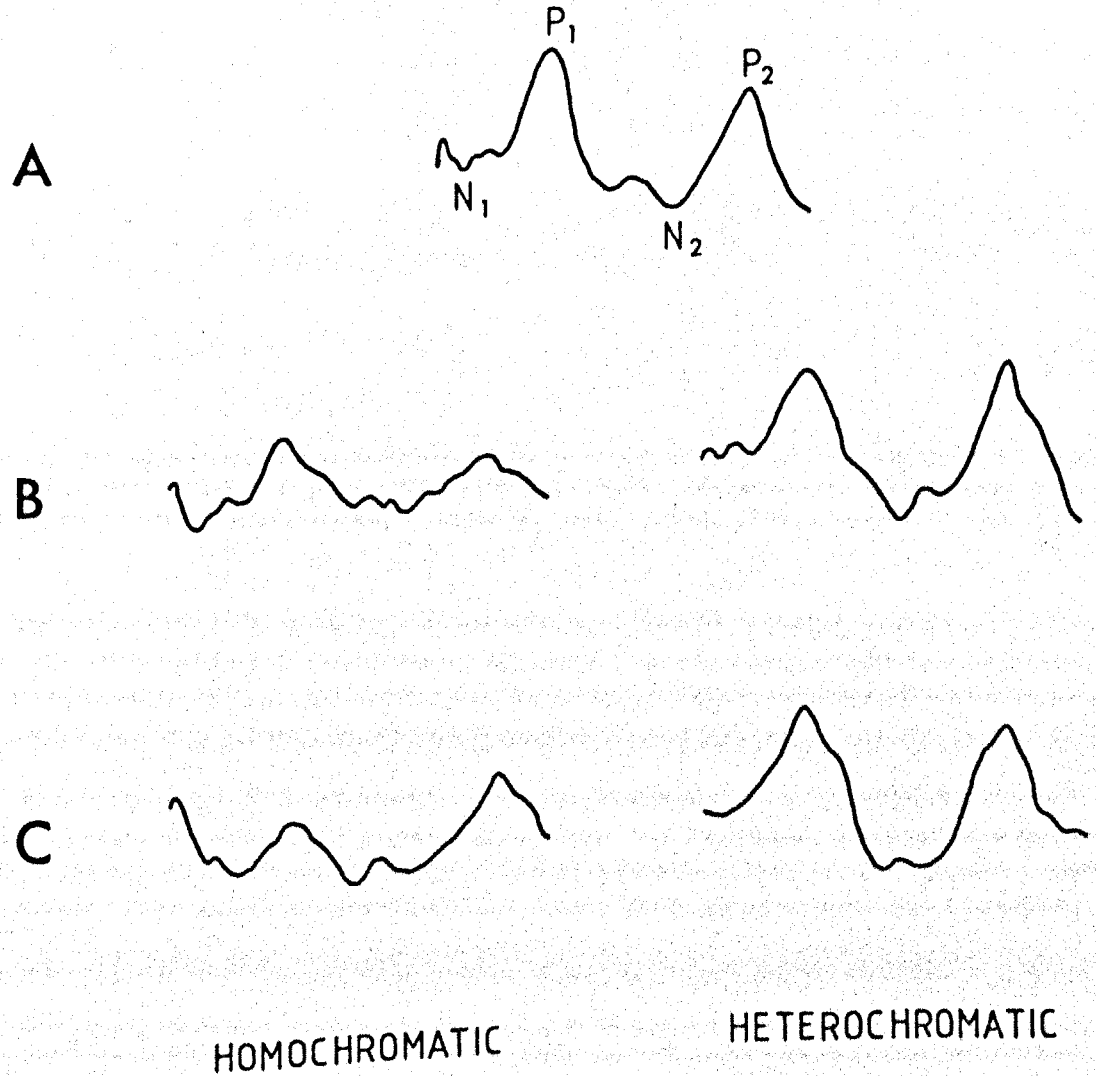
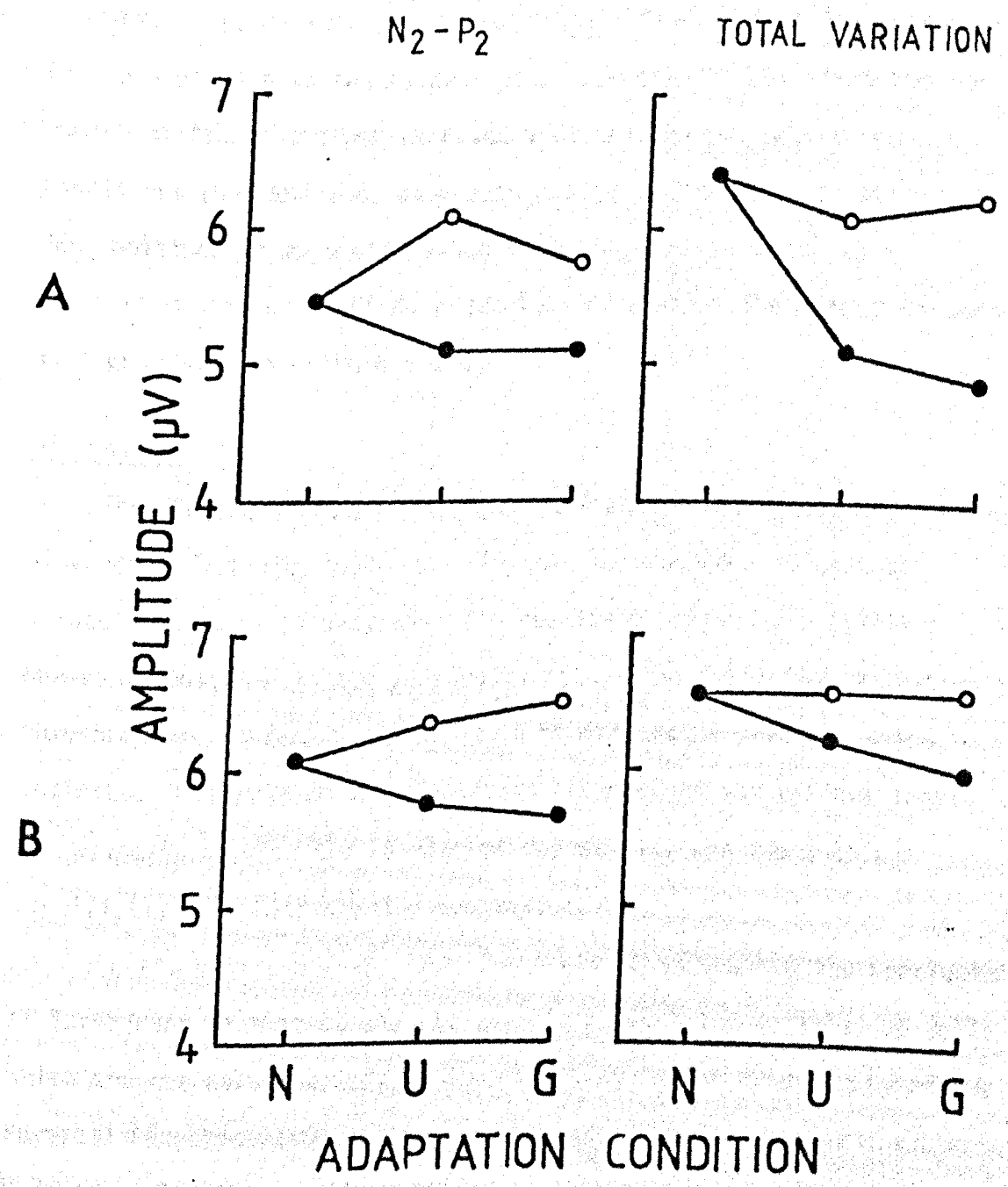

A
P1
P2
N1
N2
B
C
HOMOCHROMATIC
HETEROCHROMATIC

Fig. 27

Mean amplitude of VEP components elicited by 8Hz phase reversal of a coloured grating of periodicity 1.0 cycles/deg (a) or 2.0 cycles/deg (b) without adaptation, following homochromatic or heterochromatic adaptation to a uniform field, and following homochromatic or heterochromatic adaptation to a grating of the same orientation and size.



N no adaptation
U uniform field adaptation
G grating adaptation
●—● homochromatic
○—○ heterochromatic

grating. Fig. 27 shows, for both spatial frequencies, the amplitudes recorded using both the methods described above. Data from the two homochromatic conditions (R-R and G-G) and the two heterochromatic conditions (R-G and G-R) have been pooled in Fig. 27. In all cases, VEP amplitude is more attenuated following homochromatic than heterochromatic adaptation, regardless of whether the adaptation pattern is a grating or a uniform field.

Discussion

The finding that, at both spatial frequencies, amplitude is more attenuated following homochromatic than heterochromatic grating adaptation, is consistent with the results of May et al. (1974). However, amplitude is almost equally attenuated following adaptation to a homochromatic uniform field and to a homochromatic grating, which indicates that much of the adaptation occurred at the retinal level. This is inconsistent with the results of May et al., who found colour specificity only with grating adaptation.

The aim of the present experiment was to strengthen the conclusion of Experiment II that CI and CII largely reflect the activity of cells which are not colour coded, by demonstrating colour specificity of the reversal response using the same equipment and one of the same subjects. Unfortunately, the results obtained in this experiment with adaptation to uniform coloured fields show that no conclusion concerning the colour sensitivity of the sources of the reversal response is justified.

CHAPTER SIX

DEPTH SPECIFICITY

6.1 Introduction

Although the image formed on the retina is a two-dimensional representation of visual space, a number of cues exist in the retinal image to the distances of objects from the viewer. Such information may be derived from interposition cues, from motion parallax and from the relative sizes of the images of identifiable objects. However, interposition cues do not provide quantitative depth information, while motion parallax and image size cues depend upon image motion and knowledge of absolute object size, respectively. When the overlapping images of the two retinae are combined, however, precise depth cues which are independent of such variables arise from the magnitude and direction of horizontal disparities in the relative positions of images on the two retinae. A compelling illusionof depth can be easily created by presenting a pair of such disparate two-dimensional images, one to each eye (e.g. Julesz, 1964, 1971).

Stereoscopic depth perception is thought to be mediated by binocularly driven cells in the visual cortex which are selectively sensitive to narrow ranges of horizontal disparity. Single-unit recordings from such cells have been made in the striate cortex of both the cat (Barlow, Blakemore and Pettigrew, 1967; Nikara, Bishop and Pettigrew, 1968; Josuah and Bishop, 1970) and monkey (Poggio and Fischer, 1977; but see Hubel and Wiesel, 1970, 1973), and also in the prestriate cortex of the monkey (Hubel and Wiesel, 1970; Poggio and Fischer, 1977).

A considerable body of psychophysical evidence exists for the existence of disparity-sensitive cells in man. Stereoscopic depth can be accurately detected in a pair of binocularly presented two-dimensional patterns over a wide range of retinal disparities (e.g. Blakemore, 1970; Richards and Foley, 1971). In addition, a depth percept can be created

by simulating the interocular delay which occurs when the eye scans a scene containing objects at different depths (Ross, 1974; Tyler, 1974). Aftereffect and illusion paradigms (reviewed in section 1.3) have been used to show that both prior and simultaneous exposure to a binocularly presented pattern carrying one particular retinal disparity affects the apparent depth position of a target (Mitchell and Baker, 1973; Richards, 1972), and that greater elevation of the detection threshold of a target occurs following adaptation to a pattern carrying a similar retinal disparity than to one carrying a different disparity (Blakemore and Hague, 1972; Felton, Richards and Smith, 1972). These authors have interpreted their findings in terms of adaptation of and inhibition between cortical cells tuned to narrow ranges of disparities.

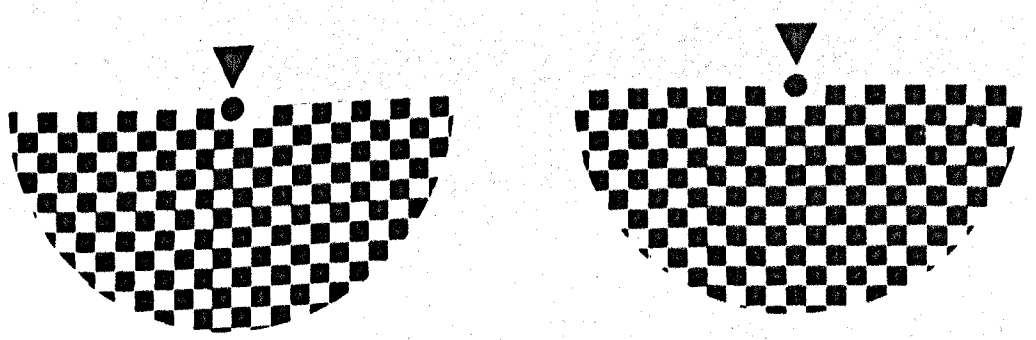
Evoked potential evidence of disparity-sensitive cells in the human visual cortex also exists. Fiorentini and Maffei (1970) have shown that the amplitude of the VEP elicited by a binocularly viewed grating reversing in phase at 8Hz is greater when the gratings presented to the two eyes are of slightly different spatial frequencies, so that the image appears inclined in depth, than when they are of the same spatial frequency. Regan and Spekreijse (1970) have used alternations in the disparity between a pair of random dot patterns to produce the impression of a square moving back and forth in depth at a frequency of 0.45Hz. They report that the depth alternations elicit a transient VEP component of latency 160ms which cannot be accounted for in terms of horizontal image displacement. Transient VEPs have also been elicited by the onset of a depth target in a binocularly viewed dynamic noise field (Lehmann and Julesz, 1978).

In this chapter, the depth specificities of VEP components CI and CII are examined by measuring the amplitude attenuation resulting from

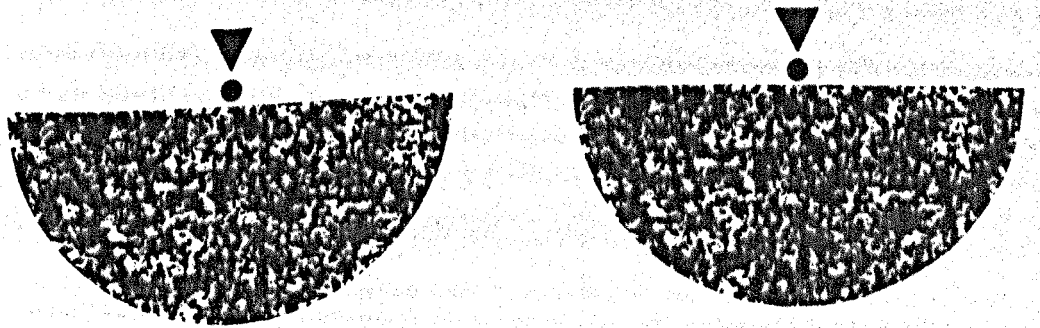
Fig. 28

Stereopairs used to elicit VEPs in Experiments 13(a) and 14(b).

A



B



adaptation to patterns carrying various binocular disparities. Attenuation of the VEP components elicited by a checkerboard and by a visual noise pattern is studied in Experiments 13 and 14 respectively.

6.2 Experiment 13: The specificity of CI and CII to the stereoscopic depth of an adapting checkerboard.

In this experiment the specificity of amplitude attenuation to the VEP components CI and CII, elicited by a checkerboard pattern, to the stereoscopic depth position of an adapting checkerboard is examined.

Procedure

Six subjects with normal or corrected acuity and normal stereoacuity were used. The stimuli, which were checkerboards of periodicity 1.0 cycles/deg, were presented in tachistoscope B. To facilitate fusion of binocularly disparate images, the small fixation cross used in earlier experiments was replaced by a central black disc subtending 0.5 deg, and a black triangle (see Fig. 28). Two adaptation patterns were simultaneously presented, one to each eye. These differed in the horizontal position of the fixation marks relative to the checkerboard, so that when the fixation marks were fused there was a horizontal disparity between the positions of the two checkerboards on the retinae, which gave rise to a depth percept. To ensure fusion, it was found necessary to increase the adaptation period from the usual 300ms (see section 2.1) to 500ms, and the interval between cycles was correspondingly increased to 1000ms to avoid the build-up of afterimages. A single stimulus pattern, viewed binocularly, was used so that the pattern always appeared in the same depth plane as the fixation marks. During the intervals between pattern presentations the subject viewed a uniform field containing only the fixation marks. A range of five adaptation disparities was used varying

Fig. 29

VEP waveforms showing the amplitudes of CI (a) and CII (b) elicited by a checkerboard without adaptation and following adaptation to a similar checkerboard presented stereoscopically to appear in front of, in the same plane as, or behind the stimulus pattern. Subject ATS.

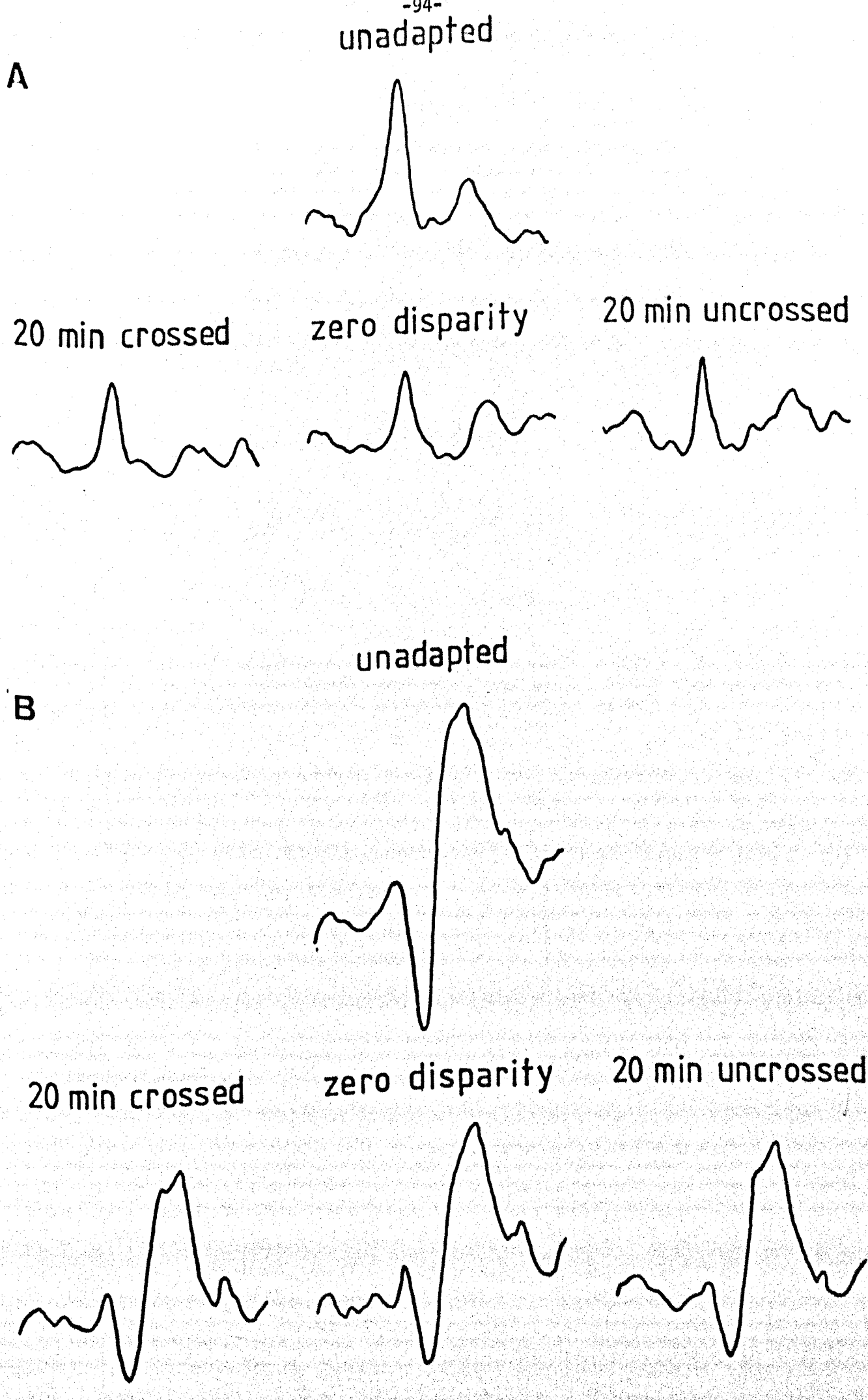
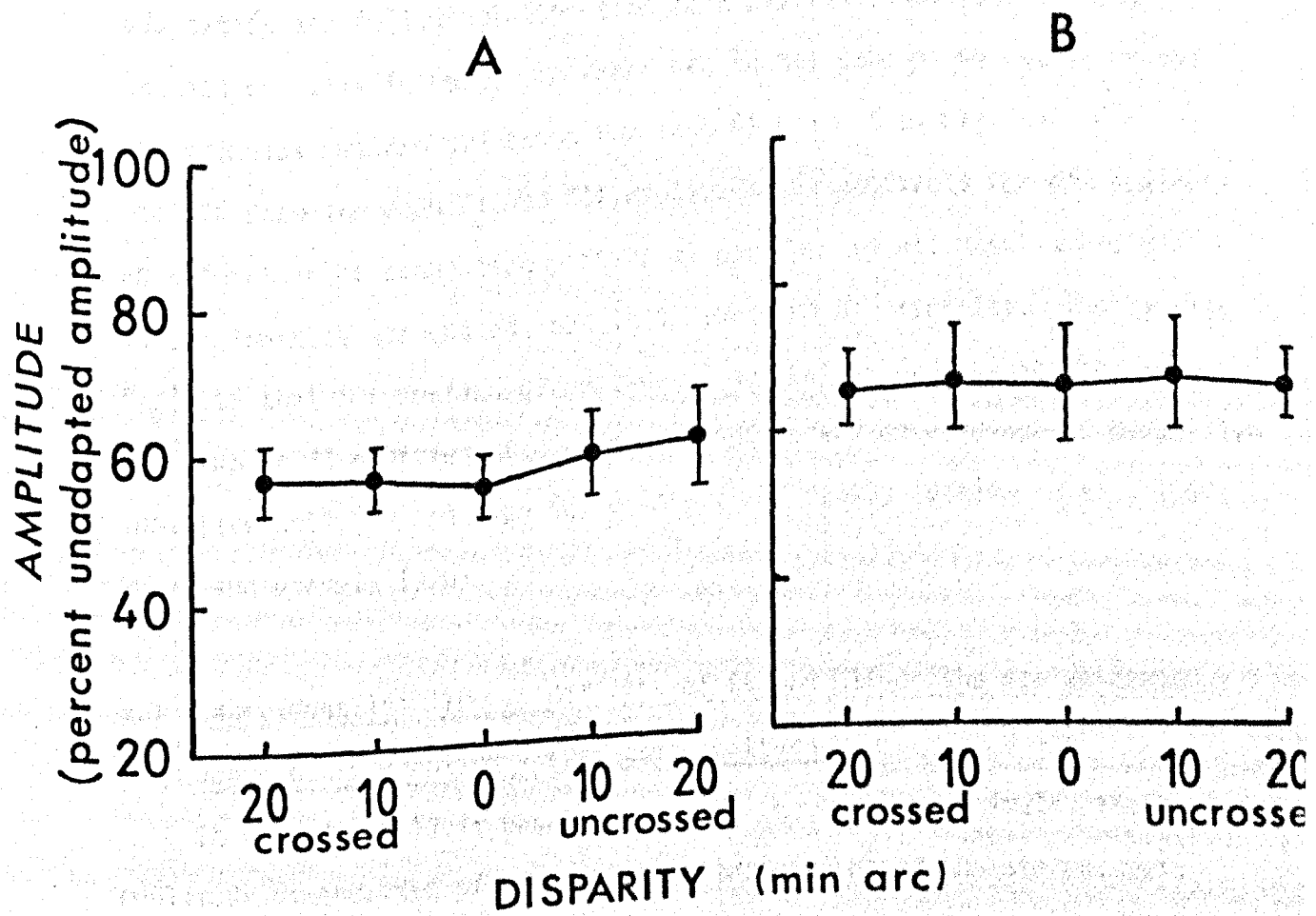

unadapted
A
20 min crossed
zero disparity
20 min uncrossed
unadapted
B
20 min crossed
zero disparity
20 min uncrossed

Fig. 30

Mean CI (a) and CII (b) amplitudes elicited by a checkerboard stimulus as a function of the retinal disparity of an adaptation checkerboard of the same orientation and size.


A
B
AMPLITUDE
(percent unadapted amplitude)
100
80
60
40
20
20 10 0 10 20
crossed
uncrossed
20 10 0 10 20
crossed
uncrosse
DISPARITY (min arc)

from 20 min crossed disparity (pattern in front of fixation plane) through zero disparity to 20 min uncrossed disparity (behind fixation plane); VEPs were also recorded in the absence of adaptation.

Results and Discussion

The VEP waveforms elicited by a checkerboard in the absence of adaptation and following adaptation to a similar checkerboard presented stereoscopically to appear in front of, in the same plane as, or behind the stimulus pattern are shown for both CI and CII in Fig. 29. Figs 30a and 30b show the mean CI and CII amplitudes respectively for all subjects as a function of adaptation pattern disparity. In all cases amplitude is considerable attenuated, but is independent of disparity. The results indicate that attenuation of neither CI nor CII is depth-specific, at least up to disparities of 20 min arc, and reveal no evidence of disparity-sensitive cells of the type found in cat and monkey (Barlow et al., 1967; Hubel and Wiesel, 1970).

6.3 Experiment 14: The specificity of CI and CII to the stereoscopic depth of an adapting visual noise pattern

In Experiment 13 it was found, using checkerboard stimuli, that amplitude attenuation of CI and CII is independent of the stereoscopic disparity of an adapting pattern. However, since the disparity which can be obtained is limited by the check size, and the check size is limited by the fact that VEP amplitude decreases with very large check size (see section 4.2) it was only possible to measure attenuation caused by adaptation to patterns carrying up to 20 min disparity. It was therefore decided to repeat the experiment using visual noise patterns which, if the pattern elements are of appropriate size, elicit large CI and CII

components and, because of the irregularity of the pattern, can be fused at much greater disparities.

Procedure

The same four subjects used in Experiment 13 were used in Experiment 14. The procedure was the same as for Experiment 13, except that visual noise patterns (illustrated in Fig. 28b) were used, and the five adaptation disparities used ranged from 40 min crossed to 40 min uncrossed disparity in 20 min steps.

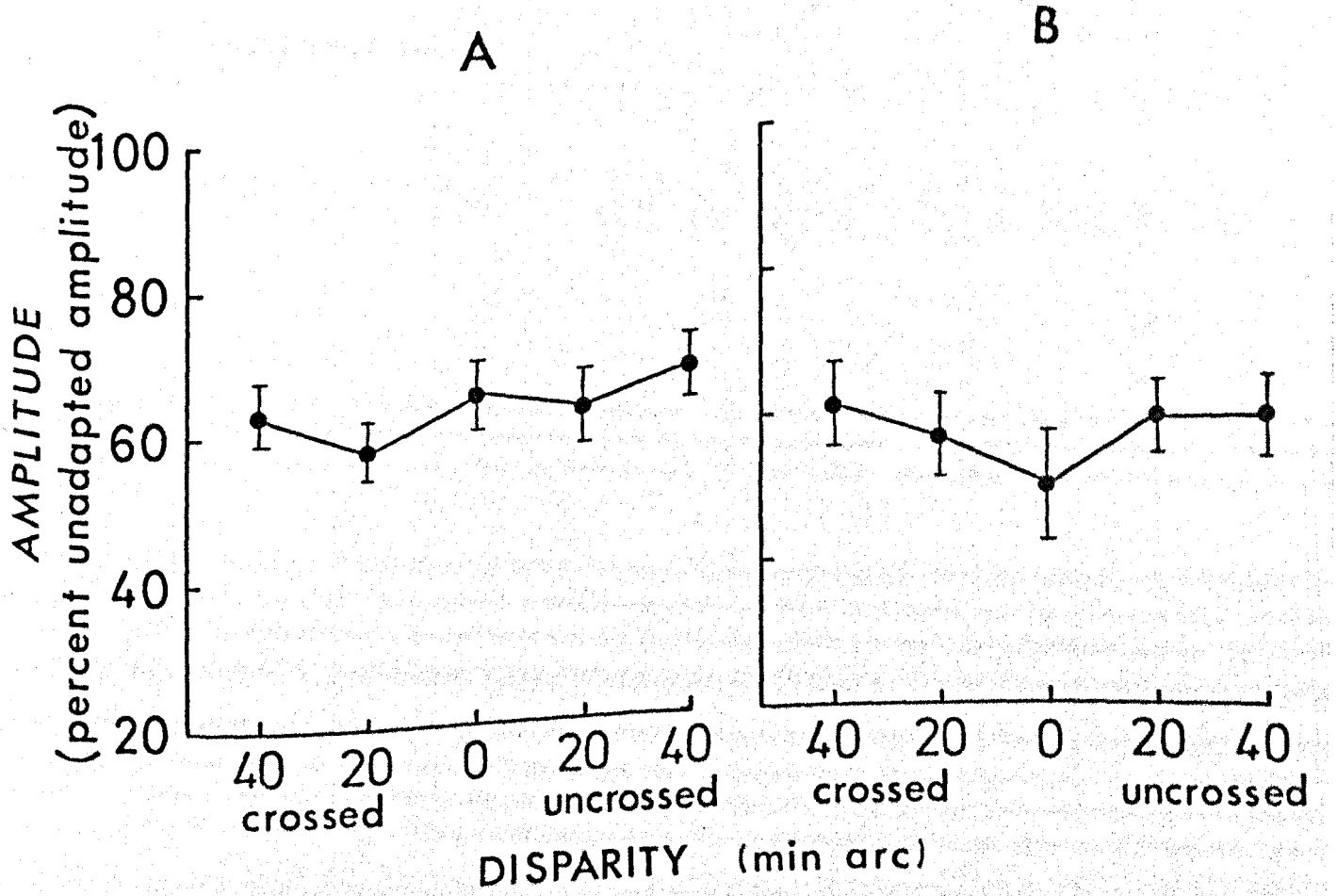
Results and Discussion

Figs. 31a and 31b show the mean CI and CII amplitudes respectively as a function of adaptation pattern disparity. As in the previous experiment, amplitude is considerably attenuated in all cases but is independent of disparity.

The results extend the conclusion of Experiment 13, that attenuation of neither CI nor CII is depth specific, to disparities of up to 40 min crossed or uncrossed. Although stereopsis is possible with much larger disparities (e.g. Blakemore, 1970), this figure corresponds to a considerable difference in apparent depth between adaptation and test patterns and is larger than that required to demonstrate depth-specific psychophysical threshold elevation (Blakemore and Hague, 1972). This suggests that the sources of CI and CII do not include disparity-sensitive cells of the type which are thought to mediate such threshold elevation. In the case of CI, thought to arise in striate cortex, this is consistent with the failure of Hubel and Wiesel (1970) to find binocular depth cells in macaque monkey striate cortex, but inconsistent with the conflicting report of Poggio and Fischer (1977) that most cells in monkey foveal striate cortex are depth-sensitive. In the case of CII, thought to arise

Fig. 31

Mean CI (a) and CII (b) amplitudes elicited by a visual noise stimulus as a function of the retinal disparity of a similar adaptation pattern.


A
B
AMPLITUDE
(percent unadapted amplitude)
100
80
60
40
20
40 20 0 20 40
crossed
uncrossed
DISPARITY (min arc)

in prestriate cortex depth sensitivity might have been expected since both the above authors report that depth-sensitive cells are common in monkey prestriate cortex. The lack of depth-specificity of CII may perhaps be explained in terms of Zeki's (1974, 1978a) notion of the division of prestriate cortex into a number of anatomically and functionally distinct regions, of which perhaps only one is specialized for depth processing.

CHAPTER SEVEN

CONCLUSIONS

There is a large body of evidence suggesting that cells in the mammalian visual system are selectively sensitive to specific characteristics of the visual input. This evidence derives from two main sources: electrical recordings taken from single units at various locations in the cat and monkey visual systems, and psychophysical adaptation studies in humans.

In section 1.3 psychophysical and neurophysiological evidence was reviewed which suggests that there exist a number of primary stimulus dimensions or attributes in terms of which visual information is encoded, namely orientation, size, colour, depth and direction and velocity of motion. It was suggested that each cell responds selectively to a narrow range of values on one or more of these stimulus dimensions, while failing to discriminate between values on other dimensions. Thus any particular cell might respond to a line of any colour, provided its orientation falls within a particular range, or to a line of any orientation provided it moves in a particular direction. The visual system may therefore be viewed as a system of largely independent channels, each concerned with a particular range of values on a particular stimulus dimension.

The primary aim of the research presented in this thesis has been to provide a link between human psychophysical and mammalian neurophysiological data. This reconciliation may be viewed as comprising two separate stages: the demonstration of parallels between human and sub-human physiology, and the reconciliation of human psychophysics with human physiology. Because of the impracticality of obtaining single-unit recordings from human subjects, psychophysical evidence has often been explained in terms of the known neurophysiological properties of the cat or monkey visual system, and the important intermediate step has been overlooked. The strategy

employed in this thesis has been to apply a psychophysical adaptation procedure to a human physiological measure, namely the pattern-onset related VEP components CI and CII (first described by Jeffreys), in an attempt to provide the missing link. By comparing the stimulus specificities of CI and CII (as revealed by adaptation) with those of single units or channels in sub-human species, it was hoped to provide parallels between human and sub-human visual physiology. Secondly, since the likely origins of the VEP components under investigation are known (see section 1.2), it was hoped to relate certain psychophysical adaptation effects to activity in specific regions of the visual cortex by comparing psychophysical tuning functions obtained, for example, by measuring threshold elevation, with VEP tuning functions obtained by measuring amplitude attenuation. The degree of progress made towards achieving these aims will now be discussed.

In chapter 3 the orientation specificity of the attenuation of CI and CII which occurs following adaptation was examined. In the case of CI, believed to originate in striate cortex (see section 1.2), it was clearly shown that with grating stimuli the degree of attenuation is dependent on the orientation of the adaptation pattern. This effect may be explained by assuming that most of the cells contributing to CI respond only to stimuli of a particular orientation and only become adapted following exposure to a pattern of that orientation. This would suggest that the predominance of orientation-sensitive units found in cat and monkey striate cortex (e.g. Hubel and Wiesel, 1962, 1968) also occurs in human striate cortex. In the case of CII, believed to originate in prestriate cortex, orientation specificity could not reliably be studied using gratings since CII is relatively insensitive to such stimuli. However, using checkerboard stimuli an orientation tuning function was

obtained which, although not significant, was as pronounced as that for CI recorded under similar conditions. It is therefore possible that the source of CII also comprises largely orientation-sensitive cells, as do the prestriate regions of the cat (e.g. Hubel and Wiesel, 1965) and monkey (e.g. Zeki, 1978b) visual cortex.

The adaptation procedure used in these experiments, in which the VEP amplitude elicited by a stimulus pattern of invariant orientation was recorded following exposure to each of a range of adaptation patterns of different orientations, was designed to allow direct comparison of the results with psychophysical adaptation experiments employing a similar paradigm. Such a comparison reveals that the tuning functions are similar in the two cases, suggesting that the two effects are mediated by the same cells. It may therefore be concluded that orientation-specific psychophysical threshold elevation occurs in the striate cortex, although adaptation may also occur in non-oriented units in the retina and lateral geniculate nucleus. Thus, in the case of orientation specificity, the adaptational properties of CI provide a link between the organization of human striate cortex and both human psychophysics and sub-human physiology.

Also in Chapter 3 an attempt was made to link knowledge of meridional differences in acuity deriving from single unit recordings from cat striate cortex with that deriving from human acuity measures, by studying meridional variations in the amplitude of CI elicited by a grating. However no such differences were recorded; the probable reasons for this are discussed in section 3.5.

A similar rationale underlies the experiments presented in Chapter 4, in which size specificity was examined. The sensitivity of CI, CII and CIII to checkerboards of various sizes was first examined, and sensitivity functions were plotted which could be compared with psychophysical

contrast sensitivity functions. The amplitude of all three components is maximal when elicited by a checkerboard of periodicity 2.0 cycles/deg, and decreases progressively with higher and lower periodicities. This figure is about half an octave lower than that usually quoted for maximum contrast sensitivity, which occurs at about 3.0 cycles/deg (e.g. Campbell and Robson, 1968). However the functions are in other respects very similar. Like the contrast sensitivity function, VEP amplitude sensitivity declines to half strength at about three octaves above the optimum periodicity, but declines rather more slowly with smaller check sizes.

Having established the optimal check size, further experiments were conducted in which the VEP amplitude elicited by an invariant stimulus pattern was measured as a function of the periodicity of an adaptation pattern. Both CI and CII were found to show specificity to the size of the adaptation pattern, provided the adaptation pattern was of a type (e.g. a checkerboard) to which the components are sensitive. This may be explained by assuming that most of the cells contributing to CI and CII respond only to stimuli of a particular periodicity or size, and become adapted only following exposure to a pattern of that size. This in turn suggests that the size-sensitive cells found in cat and monkey visual cortex (e.g. Campbell, Cooper and Enroth-Cugell, 1969; Campbell, Cooper, Robson and Sachs, 1969) occur also in both striate and prestriate regions of human visual cortex. The size tuning functions obtained for attenuation both of CI and of CII are similar to those found in psychophysical threshold elevation (e.g. Blakemore and Campbell, 1969), suggesting that the two effects are mediated by the same cells. Since CI is believed to originate in striate cortex, it may be concluded that size-specific threshold elevation is mediated by cells in striate cortex, although adaptation may also occur in more peripheral regions.

Also in Chapter 4 an experiment was described in which attenuation of CI was used to provide physiological data consistent with the psychophysical finding that greater adaptation occurs at the orientations of the fundamental Fourier components of an adapting pattern than at the orientations of the edges contained in the pattern. The result of this experiment was not interpreted as evidence of spatial Fourier analysis in the visual system; instead it was suggested that it may reflect the activity of channels sensitive to spatial luminance periodicities. Obviously further research would be required to test this hypothesis; the object of Experiment 8 was merely to link the psychophysical finding outlined above with physiological measures, and not to resolve the current controversy concerning visual Fourier analysis.

Finally in Chapter 4 two experiments were presented in which interocular transfer of VEP attenuation was examined. In the first it was shown that attenuation of VEP amplitude partially transfers interocularly. This finding is in agreement with studies of interocular transfer of psychophysical adaptation effects (e.g. Blakemore and Campbell, 1969) and also with physiological evidence that most cells in cat and monkey visual cortex are binocularly driven (e.g. Hubel and Wiesel, 1962), and therefore provides a link between the two. In the second experiment the degree of interocular transfer of CI and of CII was compared, and it was concluded that the greater degree of binocularity found in prestriate cortex than in striate cortex of the monkey (Baker et al., 1974) may also be true of man.

In Chapters 5 and 6 the specificity of VEP amplitude attenuation to the colour and depth, respectively, of an adapting pattern was examined. It was expected that CI, at least, would show specificity to both colour and depth, since a substantial number of colour-coded and depth-sensitive

cells exist in monkey striate cortex (e.g. Hubel and Wiesel, 1968; Poggio and Fischer, 1977), and the existence of such cells is suggested by the specificity to both colour and depth of psychophysical adaptation effects (e.g. McCollough, 1965; Felton, Richards and Smith, 1972). However, neither CI nor CII showed specificity either to colour or to depth. The lack of colour specificity of CII may be explained in terms of Zeki's (e.g. 1974) notion of functional specialization of prestriate cortex, in which only one area (V4) contains colour-coded cells, while another (possibly V2 or V3, see Jeffreys, 1978) gives rise to CII. The lack of colour specificity of CI and the lack of depth specificity of CI and CII are difficult to reconcile with monkey single unit data obtained by Zeki and others, although it should not be assumed that human prestriate cortex has the same functional subdivisions as the rhesus monkey (Allman and Kass (1975) have reported significant differences between owl monkey and rhesus monkey in this respect, and further variations in man are possible). It may be that these negative findings simply indicate that the procedure used was not sufficiently sensitive to detect amplitude differences resulting from adaptation of a relatively small number of colour-coded or disparity-sensitive cells.

It can be seen from this summary of findings that, in the case of orientation and size specificity at least, the study of CI and CII has provided support for the interpretation of psychophysical adaptation effects in terms of the activity of cortical cells of the type found in cat and monkey. However, the validity of any such support derived from the study of VEPs is dependent on the validity of the underlying assumptions concerning the sources of those VEPs. Several such assumptions have been implicitly made throughout this thesis; these will now be briefly discussed.

Evoked potential studies have often been criticised on the grounds that meaningful interpretation of VEPs is not possible in the absence of detailed knowledge of the relationship between gross potentials recorded at the scalp and the characteristics of individual neurones. Discussion of this relationship has centred on the question of whether gross surface potentials arise from graded dendritic potentials or from axon spikes. Some authors have argued that surface potentials result from temporal summation of brief (1-2ms) axon spikes (e.g. Bishop, 1936) or of longer-lived (10-100ms) spikes (Adrian and Matthews, 1934) from a large number of neurones. Others (e.g. Purpura, 1959; Li, 1963) have argued instead that VEPs can be accounted for in terms of summation of the relatively slow postsynaptic (dendritic) potential changes generated by individual neurones. Fox and O'Brien (1965) have demonstrated a very close correspondence between the evoked potential waveform and the firing rate of a single neuron in the visual cortex. However this relationship may not be causal; in view of the close correspondence between axon firing rate and dendritic activity, it is not clear whether the evoked potential results from temporal summation of spikes or whether both the evoked potential and the axon spikes result from dendritic activity.

Although the exact nature of the sources of VEPs is not fully understood, this is a question which is not central to the interpretation of the results presented in this thesis. More central to the validity of the conclusions drawn in the preceding chapters is the assumption that CI originates in striate cortex while CII originates in prestriate cortex. If this assumption is valid it is of little importance whether the sources of CI and CII are postsynaptic potentials, action potentials, or a combination of the two. The model on which Jeffreys' derivations (Jeffreys, 1971; Jeffreys and Axford, 1972a,b) of the origins of CI and

CII is based assumes that the cortex may be considered as a dipole sheet within a volume conducting brain, the dipole axis being perpendicular to the surface of the cortex. The validity of these assumptions has not been proved directly, although several studies have shown that models based on these assumptions have considerable predictive power. Vaughan, Costa and Ritter (1968), for example, recorded surface potentials over the motor cortex which were evoked by asking the subject to contract the muscles of various parts of the body. Because of the topographic organization of the motor cortex the probable sources of these potentials were known with some accuracy. The scalp distribution of the potential evoked by each set of muscles was consistent with the supposition that the motor region innervating those muscles was acting as a dipole source within a volume conducting brain. Regan (1972, p21) has pointed out that the organization of the visual cortex is less regular and simple than that of the motor cortex so that the extension of the dipole model to the visual cortex may not be straightforward. However the finding (Vaughan and Ritter, 1970) that the auditory potential recorded at the vertex has a scalp distribution consistent with a dipole source in primary auditory cortex suggests that the model can in fact be extended to sources in sensory cortex.

Although studies of this kind provide sufficient support for the dipole model to justify its continued use in the interpretation of the properties of CI and CII, it cannot be stated categorically that the sources of these components are those proposed by Jeffreys. There is therefore a need for direct evidence concerning these sources. Such evidence should ideally come from studies of patients with damage to part of the visual cortex. Damage to, for example, prestriate cortex on the upper surface of the right occipital lobe would be expected to selectively

impair the amplitude of CII elicited by a stimulus in the lower left quadrant of the visual field, while leaving CI unaffected. Evidence of this kind might also be derived from the effects of lesions of the visual cortex of monkeys; however it would first be necessary to confirm the existence of CI and CII in monkeys. Attempts to record these components in the cat have been unsuccessful (James and Jeffreys, personal communication), possibly because of the effect of anaesthesia. However, in view of the close correspondence between the anatomy of the visual cortex in man and in monkey, it would be surprising if CI and CII could not be recorded from awake monkeys under appropriate stimulation and recording conditions. In view of the limited opportunities for adequate study of the effects of lesions in man, the most promising source of direct evidence concerning the sources of CI and CII would seem to be studies involving lesions of the visual cortex in monkeys.

Notwithstanding the reservations discussed above, present indications suggest that the assumption that CI and CII arise in striate and prestriate cortex respectively is justified. Attempts have been made in the past to provide support for the interpretation of psychophysical adaptation effects in terms of the activity of cortical cells of the type found in cat and monkey by measuring other types of VEP. However, many of these attempts have been hampered by a lack of knowledge of the sources of the VEPs being measured. The onset-related components CI and CII are unusual in that they have distinct sources in separate regions of visual cortex, and can be studied independently by means of selective enhancement techniques (see section 1.2). This knowledge of sources allows meaningful interpretation of VEP correlates of psychophysical findings, and allows such psychophysical effects to be localized rather than merely correlated with a VEP measure whose origin and significance are obscure. The bulk

of existing VEP literature consists of descriptive studies which reveal no new knowledge of the mechanisms of visual processing. Only when an attempt is made to determine the anatomical (e.g. Jeffreys, 1971; Halliday and Michael, 1970) or functional (e.g. Kulikowski, 1977) nature of the sources of VEP components can descriptions of components be used to gain new insight into visual processing.

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